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New species of Agathidiini from Far East with taxonomic and distributional data about Leiodinae from Middle Asia (Coleoptera: Leiodidae)

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Abstract *Stetholiodes puetzi* sp n. and *Agathidium* (*Neoceble*) *shannae* sp n are described, *Trichohydnobius* Vogt, 1961 is newly proposed for the subgenus of *Sogda* Lopatin, 1961, *Sogda pavlovskii* Lopatin, 1961 from Turkmenistan, *Leiodes subtilis* Reitter, 1885 from Kazakhstan and *Liocyrtusa minuta* (Ahrens, 1812) from Kyrgyzstan are recorded from these countries for the first time.

Taxonomy, descriptions, distribution, Coleoptera, Leiodidae, Palaearctic region

INTRODUCTION

Through the kindness of Andreas Pütz, Eisenhüttenstadt (Germany) and Ottó Merkl, (HNHM) we could study small but interesting leiodid material from Middle Asia and Far East. Material consists of species of genera *Sogda* Lopatin, 1961, *Leiodes* Latreille, 1802, *Liocyrtusa* Daffner, 1982, *Stetholiodes* Fall, 1910, and *Agathidium* Panzer, 1797. Two of the species are new for science and two species are new for Turkmenistan, Kyrgyzstan and Kazakhstan. Material is deposited in Švec's collection (SC), Angelini's coll. (AC), Pütz's coll. (PC) and in the coll. of Hungarian Natural History Museum Budapest (HNHM). Other abbreviations used in the work are as follows: ratio of width . length = W/L, ratio of width : height = W/H.

The monograph of the palaearctic *Agathidium* was given by Angelini (1995) and include also the species from Far East. Other taxonomic or faunistic studies concerning the species of the genus *Sogda, Leiodes* and *Liocyrtusa* were presented by Daffner (1983), Perkovsky (1988) and Švec (1996). The papers about *Stetholiodes* were given by Angelini (1987) and Perkovsky (1990).

RESULTS

Stetholiodes puetzi sp. n.
(Figs 1–5)

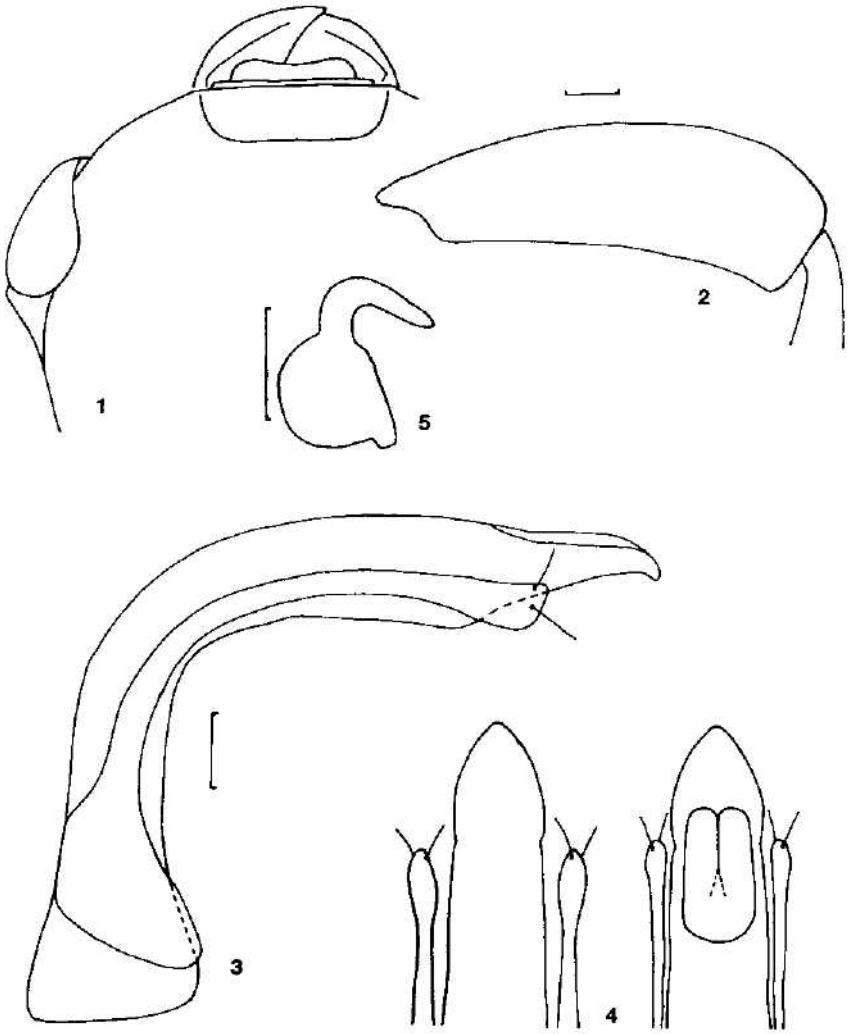
TYPE MATERIAL Holotype, male "Russia, Siberia, Primorskij kraj, Partizansk. distr., Alexeyevsky Khreb., 20 Km E of Sergeyevka, Forest Andreyevka river, 400 m, 26 - 29 VII 1993, Putz & Wrase leg.", deposited in PC, paratypes 3 males and 2 females, PC, 2 males and 1 female, AC, the same locality and collectors

Length of body 3.2–4.0 mm, in holotype 4.0 mm, head 0.8 mm, pronotum 1.1 mm, elytra 2.1 mm, width of head 0.5 mm, pronotum 1.8 mm, elytra 1.8 mm, height of pronotum 1.1 mm, elytra 0.9 mm.

Dorsum uniformly black; mesosternum reddish-brown, metasternum black; antennae testaceous with club infuscated; legs red-brown. Dorsal surface without microreticulation except of striate clypeus. Punctures clearly visible on whole dorsum, double on head and pronotum, elytra with traces of seriate punctures. Sutural striae well developed, reaching to the 2nd third of elytral length.

HEAD. Clypeus striate. Larger punctures on head well impressed, spaced by 0.5–1 times their own diameter, the smaller ones well impressed, spaced by 1–4 times their own diameter. Antero-lateral margins rounded, clypeus not excavate, straight. Clypeal line superficial. Eyes prominent laterally. Head widest just behind eyes, temples very short (Fig. 1). 3rd antennal segment 1.8 times as long as the 2nd one and shorter than 4th+5th together.

PRONOTUM. Puncturation equal to those on head. Pronotum 1.5 times as broad as head, broader than long (W/L) = 1.63 and moderately convex (W/H = 1.70). Anterior margin slightly emarginated, lateral outline broadly rounded.

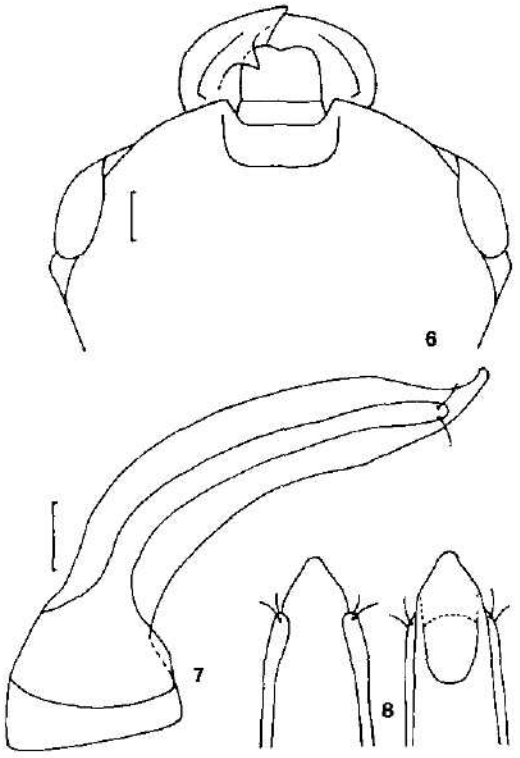


Figs 1–5. *Stetholioder puetzi* sp. n., 1 – head, 2 – male hind femora, 3, 4 – aedeagus in lateral, dorsal and ventral view, 5 – spermatheca. Scale bars = 0.1 mm.

ELYTRA. With traces of punctate rows consisting of punctures larger than those in intervals. Intervals of badly traceable rows with irregularly distributed punctures little larger than those on head. Interval punctures spaced by 0,5–1,0 times their own diameter. Elytra as wide as pronotum, longer than broad (W/L= 0.85) and a little convex (W/H = 2.0). Lateral outlines with slight humeral angle.
MESO- AND METASTERNUM. Median carina sharp, lateral lines complete, femoral lines absent. Metathoracic wings fully developed.
LEGS. Male hind femora with edge at posterior margin (Fig. 2). Tarsal formula in male 5–5–4, in female 5–4–4.
AEDAGUS. As in Figs 3, 4
SPERMATHECA. As in Fig. 5.
DERIVATIO NOMINIS. Derivated from the name of the collector.
DIFFERENTIAL DIAGNOSIS. *Stetholiodes puetzi* sp. n. clearly differs from all other known species of the genus by lacking of distinctly visible punctured elytral rows.

Agathidium (Neoceble) shannae sp. n.
(Figs 6–8)

TYPE MATERIAL. Holotype, male: "Russia, Siberia, Far East, Primorskij kraj, Lasovskij distr., Mt. Sestra, 1500–1600 m, 20 Km NO of Laso, 7.–11 IX 1994, Sundukov leg.", AC.



Figs 6–8 *Agathidium (Neoceble) shannae* sp. n., 6 – head, 7, 8 – aedeagus in lateral, dorsal and ventral view. Scale bars = 0.1 mm

Length of body 3.1 mm, head 0.7 mm, pronotum 0.8 mm, elytra 1.6 mm, width of head 1.0 mm, pronotum 1.4 mm, elytra 1.6 mm, height of pronotum 0.7 mm, elytra 1.0 mm.

Dorsum of head black, pronotum black with red-brown margins, elytra yellow-red with black triangular basal spot, antennae testaceous with antennal club black, legs red-brown. Mesosternum red-brown, metasternum black.

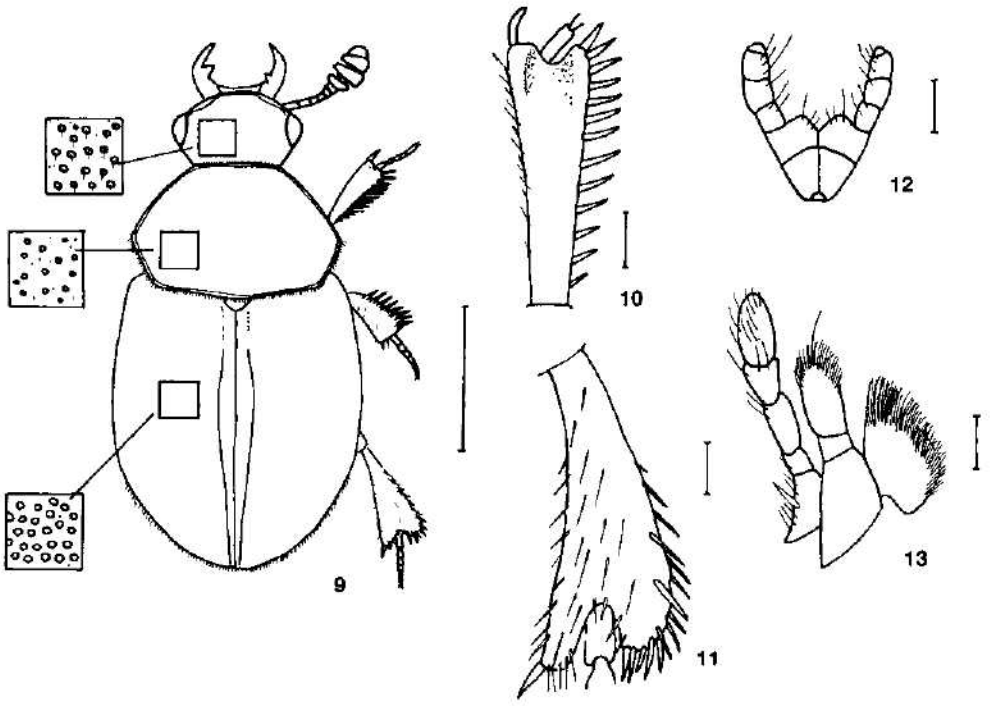
Dorsum without microsculpture. Puncturation slightly developed but clearly visible on the whole dorsum. Sutural striae distinctly developed, reaching to midlength of elytra.

HEAD. Punctures large and well impressed, spaced by 0.25 times their own diameter. Head widest just behind eyes, temples as long as the fifth of eyes length (Fig. 6). Antero-lateral margins simply rounded, clypeus slightly emarginated. Clypeal line very superficial, eyes prominent laterally. 3rd antennal segment 1.5 times as long as the 2nd one and shorter than 4th+5th together.

PRONOTUM. Puncturation similar to those on head, punctures spaced by 0.25–1 times their own diameter. 1.47 times as broad as head, moderately broader than long (W/L = 1.81) and a little convex (W/H = 1.89). Anterior margin deeply emarginated, lateral outlines broadly, distinctly rounded at basal half of length, slightly rounded in cranial half of pronotal length.

ELYTRA. Punctures larger than those on pronotum, spaced by 0.5–1 times their own diameter, rarely some smaller punctures interposed. Just a little broader than pronotum, a little longer than broad (W/L = 0.96) and moderately convex (W/H = 1.53). Lateral outlines with sharp humeral angle.

MESO- AND METASTERNUM. Median carina weak, lateral lines complete, femoral lines absent. Metathoracic wings fully developed.



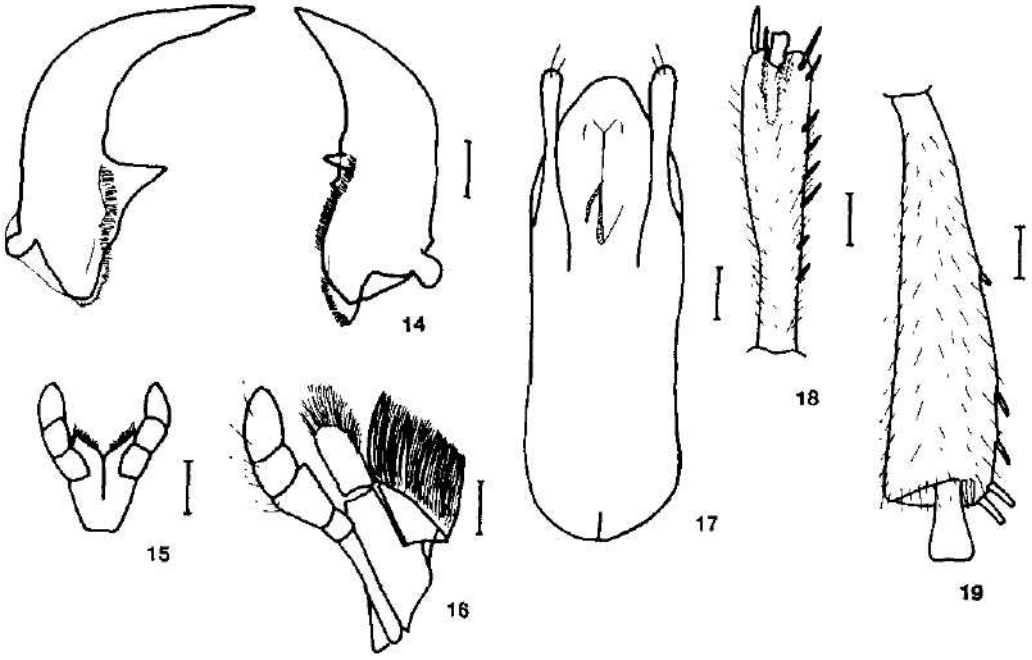
Figs 9–13. *Sogda pavlovskii* Lopatin, 9 – shape of body, 10 – anterior tibia, 11 – posterior tibia, 12 – labium, 13 – maxilla. Scale bars = 0.1 mm.

LEGS. Tarsal formula in male 5–5–4, female unknown.
AEDEAGUS. As in Figs 10, 11.
DERIVATIO NOMINIS. Following to the wishes of the collector, the new species is dedicated to his wife Shanna.
DIFFERENTIAL DIAGNOSIS. *Agathidium* (*Neoceble*) *shannae* sp. n. belongs to *A. nigripenne* group and it is very similar to *A.* (*N.*) *gurjevae* Perkovsky (1991) by shape of head and by clearly developed puncturation of whole dorsum. The new species differs from the compared species by more superficial clypeal line, colour of dorsum, and mainly by the shape of aedeagus.

Sogda pavlovskii Lopatin, 1961
(Figs 9–13, 14, 17)

MATERIAL EXAMINED. 1 male: "Turkmenia, 50 km N of Aschkabad, 100 m, 17.iv.1993, No L 88, 58°33'E, 38°22'N, M. Herblay, Gy László, A. Podluszány lgt.", HNHM; 3 females, No L 84, HNHM; 1 female, No L 84, the same *locality and collectors*, SC.

Examined specimens agree well to the original description (Lopatin 1961) as well as to the redescription given by Perkovsky (1988). Original description was based on single female. The description of the male was not publish till now. That is why we add the drawing of aedeagus as well as the shape of the body and legs (Figs 9–11, 17). Beside it there are for the first time figured mouth parts of the species (Figs 12–14).



Figs 15–19. Figs 15–18, 19 – *Trichohydnobius suturalis* Zetterstedt, 15 – labium, 16 – maxilla, 18 – anterior tibia, 19 – posterior tibia. Figs 14, 17 – *Sogda pavlovskii* Lopatin, 14 – left mandible, 17 – aedeagus. Scale bars = 0.1 mm.

DISTRIBUTION Tadzhikistan (Lopatin 1961), new record for Turkmenistan

DISCUSSION The examination of the specimens from Turkmenistan enable us to discover some characters which indicate remarkable difference between the genus *Sogda* and the taxon which was erected by Vogt (1961) under the name *Trichohydnobius* which was later synonymized with *Sogda* (Perkovsky 1988) *Trichohydnobius* was originally described as the subgenus of the genus *Hydnobius* Schmidt, 1841 Later Daffner (1983) changed the status of the taxon and proposed the name *Trichohydnobius* for the genus. Subsequently Perkovsky (1988) synonymized *Trichohydnobius* with *Sogda* In the view the fact that there are significant characters differ *Sogda* from *Trichohydnobius*, we remove the taxon *Trichohydnobius* from the synonymy here The name *Trichohydnobius* is proposed as the name of subgenus of the genus *Sogda*

Trichohydnobius Vogt, 1961 (subg. of *Sogda*) stat. n.

Trichohydnobius Vogt, 1961 142 (subg of *Hydnobius*, type species *Anisotoma suturalis* Zetterstedt, 1828)
Trichohydnobius, Daffner, 1983 23 (stated as the genus)
Trichohydnobius, Perkovsky, 1988 (synonymized with *Sogda*)

The characters differing *Trichohydnobius* from the nominotypical subgenus

	subgenus *Sogda* Lopatin, 1961	subgenus *Trichohydnobius* Vogt, 1961
1	Antennal segments 7, 9–11 distinctly asymmetrical	Antennal segments 7, 9–11 symmetrical or indistinctly asymmetrical
2	Left mandible with strongly developed sharp dens at basal half of mandible length (Fig 14)	Left mandible with strongly developed obtuse dens at the basal half of mandible length
3	Segment 2 of maxillar palpi longer than wide, the 3rd one more than twice as long as wide (Fig 13)	Segment 2 of maxillar palpi wider than long the 3rd one less than twice as wide as long (Fig 16)
4	All tibiae in both sexes short , very striking dilate and spinose with numerous long lateral spines Anterior and posterior tibiae as in Figs 10,11	All tibiae in both sexes long, of usual shape, not strongly dilated, with few short spines Anterior and posterior tibiae as in Figs 18,19
5	Tarsal grooves at anterior tibiae wide, shallow, as long as protarsi (Fig 10)	Tarsal grooves at anterior tibiae narrow, shallow, short, much shorter than protarsi (Fig 18)

Leiodes subtilis (Reitter, 1885)

Liodes subtilis Reitter, 1885 286

MATERIAL EXAMINED 1 male, "Kazakhstan, Almaty prov , 22 km N Masak, 450 m, 78°27'E, 43°13'N, 21 vi 1996, Gy Fabian, L Nadai lgt ", HMNH

DISTRIBUTION Eastern Europe, Saudi Arabia, Afghanistan, Turkmenistan, Mongolia, Siberia (Daffner 1983), new record for Kazakhstan

REFERENCES

ANGELINI F 1987 Notes on the genus Stetholiodes Fall with description of four new species (Coleoptera, Leiodidae) *Rev Suisse Zool* **94** 3–15

ANGELINI F 1995 Revisione tassonomica delle specie paleartiche del genere Agathidium Panzer (Coleoptera, Leiodidae, Agathidiini) *Monogr Mus Regional Stor Natur Torino* **18** 1–484

DAFFNER H 1983 Revision der palaarktischen Arten der Tribus Leiodini Leach (Coleoptera, Leiodidae) *Folia Entomol Hung* **44** 9–163

LOPATIN I K 1961 Novoe semejstvo jestkokrylych (Sogdiidae, fam nov) iz Tadjikistana (In Russian, Engl summary) *Izv Otd Selskohoz Biol Nauk AN Tadžik SSR* **1** 121–125

PERKOVSKY J E 1988 [Sogdidae – new synonym of Leiodidae (Coleoptera)] *Vestn Zool* **2** 65–66 (in Russian)
PERKOVSKY J E 1990 [New species of the genus Stetholiodes (Leiodidae, Coleoptera) from the Peninsula of Indochina] *Vestn Zool* **5** 63–64 (in Russian)
ŠVEC Z 1996 Leiodes stocki sp n with new faunistic records of Leiodini from the Caucasus and Central Asia (Coleoptera Leiodidae) *Acta Entomol Sloven* **4** 73–77
Vogt H 1961 Die mittel- und nordeuropaischen Arten der Gattung Hydnobius Schmidt *Entomol Bl* **57** 141–171

Acta Soc Zool Bohem **62** 84, 1998
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BOOK REVIEW

BRANDSTATTER F Die Sandrennnattern. Die Neue Brehm-Bücherei, Vol. 636. Magdeburg Westarp Wissenschaften, 1996 142 pp Softcover, ISBN 3–89432–429–5 (in German)

Another volume (Nr 636) of the Die Neue Brehm-Bucherei edition is the monograph by Dr Frank Brandstatter (head of the Zoo Neukirchen) on Afro-Asian sand-snakes of the genus *Psammophis* These elegant snakes are somewhat neglected by terrarists so far, although they belong to the commonests snakes in nature

The book summarizes in a popular scientific (and sometimes scientific) manner our current knowledge on this genus It is divided in nine chapters

The first chapter (Systematics) considers the taxonomic position of these sand-snakes Short comments are added on their evolution and phylogeny Two cladograms summarize phylogenetic relationships within the tribe Psammophini, and within the genus *Psammophis*

The second chapter (Biology of *Psammophis* species) includes the data on the nomenclature of the genus, incl a historical review, and synonymy Short descriptions are given of general anatomy and morphology, teeth and diet, form of male copulatory organs, properties and function of the poison, scales, and the fossil record

The third chapter (Ecology) summarizes the data on the life habits of *Psammophis* sand-snakes, their reproduction, diet, predators, anti-predatory mechanisms (autotomy of the tail), and parasites

Fundamentals of keeping and breeding of the sand-snakes in captivity are described in the fourth chapter (Sand-snakes in the vivarium)

The fifth chapter includes a key to the species and subspecies of the genus *Psammophis*

The most voluminous part of the book is the sixth chapter, containing descriptions of all known species and subspecies of the genus *Psammophis* The following data are given for each species and subspecies description, distribution (incl a separate map for each species), habitat, and ecology In some cases, fundamentals of breeding in captivity are presented If uncertain, relationships are discussed Latin, German, and English names are given for each species

The remaining genera of the tribe Psammophini (*Dipsina*, *Dromophis*, *Hemirhagerrhis*, *Malpolon*, *Mimophis*, *Psammophylax*, and *Rhamphiophis*) are mentioned in the seventh chapter Each genus is briefly described, incl data on the morphology, teeth, scales, life habits, distribution, etc

The eighth chapter (References) includes over 300 citations Papers containing the original species description are listed separately This is uncommon, but welcome

The ninth chapter (Appendix) is very important from the scientific point of view as it summarizes the etymology and synonymy of the scientific names of *Psammophis* species It was prepared in cooperation with M Rödl Unfortunately, some of the mentioned papers are not listed in the References section

The volume is supplemented with two color plates, and 29 black-and white figures (mostly photographs)

The book presents valuable and succinct information on this group of colubrid snakes Everybody interested in the snakes, or in the herpetofauna of Africa and Asia should purchase a personal copy

Radka Dandova

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Argoptochus pericarti sp. n. from Greece (Coleoptera: Curculionidae)

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Abstract. *Argoptochus pericarti* sp. n. is described, illustrated and compared with the related species *A. cretensis* Pic, 1904

Description, new species, Coleoptera, Curculionidae, Otiorhynchinae, Phylobiini, *Argoptochus pericarti* sp. n., Palaearctic region

The genus *Argoptochus* Weise, 1883, lastly revised by Pesarini (1980) and completed by Angelov (1987), includes 24 known species, living mainly in the Balkans and Turkey, with two species known from Italy, two species known from Central Europe and one species known from Caucasus and one species known from Siberia. The genus is represented in Greece by eight species, five of them occurring in continental part, three of them occurring in Crete and Corfu.

Our friend Jean Péricart (Montereau, France) and his colleagues P. Magnien and A. Matocq, collected in Greece, among other weevils, a new *Argoptochus* species. We dedicate this species to J. Péricart who possessed us all the specimens of the present study.

Argoptochus (*Argoptochus*) *pericarti* sp. n.
(Figs 1, 3)

TYPE MATERIAL Holotype (male), allotype (female) and 2 paratypes (males) – labelled 54 Peloponnèse, Lakonia, Vathia et env (Le Mani), 2 V 1994, Magnien, Matocq, Péricart leg. Holotype, allotype and one paratype in coll. J. Pelletier, one paratype in coll. R. Borovec.

DESCRIPTION. Body length 2.06–2.44 mm, measured from elytral apex to anterior border of eye in lateral view. Body black, the legs and antennae entirely yellow reddish.

Dorsal part of body entirely covered by adherent and raised scales. Adherent scales long, oval, pointed basally, white greyish with weak pearly shine. These scales dense on the sides of the pronotum and at a lesser degree on the lateral elytral intervals, sparse or absent from the dorsal intervals. Raised scales on head short, white greyish, not significantly prominent. Raised pronotal and elytral scales longer, white greyish on the sides and brownish on the disc. Elytral scales narrow, parallel-sided, longer than the half of width of an interval. Elytral striae with short, greyish little setae and elytral disc with hardly visible, sparse, brown, short little setae.

Rostrum 1.44–1.57× wider than long, slightly narrowed anteriad, the sides feebly concave. Dorsal surface of rostrum narrower than the half of width of rostrum itself. Eyes regularly vaulted. Head and rostrum with dense, shallow puncture.

Scape clearly curved, the first antennomere of funicle about 1.5× longer than the second one. The second antennomere conical and about 1.5× longer than wide. Antennomeres 3 to 5 about as wide as long, antennomeres 6 and 7 a bit wider than long.

Pronotum 1.16–1.26× wider than long, with sides regularly arcuated, densely punctured on disc. Disc devoid of adherent scales in its whole length.

Scutellum small, not conspicuous.

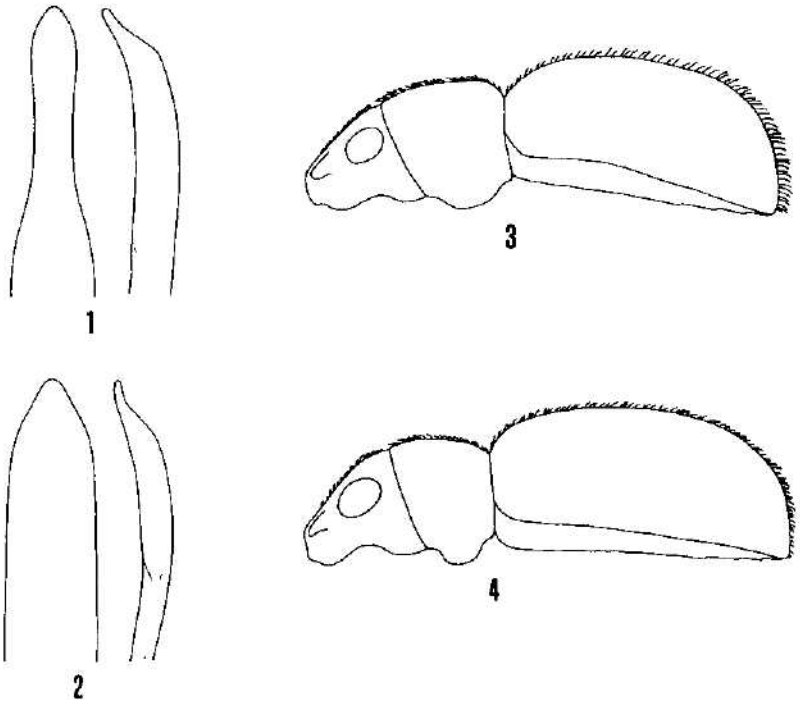
Elytra long oval, 1.27–1.38× longer than wide with regularly arcuated sides. Striae punctured, intervals shiny.

All femora toothless. First tarsomeres conical, clearly longer than wide. Second tarsomeres as long as wide. Third bilobated tarsomeres strikingly wider than the previous ones. Ungular tarsomeres exceed the third ones by about once their length. Claws free.

Aedeagus widest at its base, strongly tapered before the middle of its length, apical half narrow and consistently pointed at apex (Fig. 1).

Biology unknown.

DIFFERENTIAL DIAGNOSIS. Having yellow reddish tibiae, the long oval adherent scales, the regularly vaulted eyes, dull dorsal area of rostrum and the dense lateral bands of scales on the sides of pronotum, the new species is very similar to *Argoptochus cretensis* Pic, 1904. However, the two species can be easily distinguished by characters listed below:



Figs 1–4. Aedeagus – ventral and lateral view (1, 2) and lateral body outlines (3, 4) of: *Argoptochus pericarti* sp. n. (1, 3) and *A. cretensis* Pic (2, 4).

1. Raised scales longer than the half of width of an interval on elytra and distinct on pronotum (Fig. 3). Femora yellow reddish. Adherent elytral scales sparse. Aedeagus as in Fig 1. Peloponnesos 2 1–2 4 mm. ... *A pericarti* sp. n.
– Raised scales on elytra strikingly shorter than the half of width of an elytral interval, hardly visible on pronotum (Fig 4) Middle part of femora black. Adherent scales on elytra dense. Aedeagus as in Fig 2 Crete 2 0–2.8 mm . *A cretensis* Pic, 1904

In addition, the shape of aedeagus in *A. pericarti* sp. n. is also quite different from all other known species of *Argoptochus*.

REFERENCES

ANGELOV P 1987 Die bulgarischen Argoptochus-Arten, mit Beschreibung zweier neuer Spezies (Coleoptera, Curculionidae). *Reichenbachia* **24** 109–114

PESARINI C 1980 Le species Palearticbe occidentali della tribù Phyllobiini (Coleoptera, Curculionidae). *Boll Zool Agr Bachicoltore* **15**(1979). 49–230.

Acta Soc Zool Bohem **62** 89–100 1998
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Seven new species and new records of *Leistus* from Sichuan (Coleoptera: Carabidae: Nebriini)

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Abstract Seven new species of *Leistus* Froehlig, 1799, all from Sichuan (China) are described and illustrated *L (Leistus) cavazzutii* sp n , *L (Evanoleistus) facchinii* sp n , *L (E) haisishanicus* sp n , *L (E) miroslavae* sp n , *L (E) wolong* sp n , *L (E) wraseri* sp n , *L (E) zamotajlovi* sp n In addition, new distributional data of the following species of *Leistus* are presented *L (Leistus) ludmilae* Dvořak 1994, *L (Evanoleistus) haeckeli* Farkač 1995, *L (E) kangdingensis* Farkač, 1995 *L (E) saueri* Sciaky, 1994, *L (E) shuamaluko* Farkač 1995 (all from Sichuan) Holotypes of *L (Leistus) cyclocerus* Tschitscherine 1903, *L (Evanoleistus) cronifer* Tschitscherine, 1903, *L (E) gracilentus* Tschitschérine, 1903, *L (E) gracillimus* Tschitscherine, 1903, *L (E) nubicola* Tschitscherine, 1903 are illustrated

Taxonomy, new species, new records, Coleoptera, Carabidae, *Leistus*, Palaearctic region

In this paper, which is based on the study of numerous material and on complete literature survey (Tschitscherine 1903, Wu 1937, Dvořák 1994, Perrault 1980, 1985 and 1994, Sciaky 1994, 1995, Farkač 1995) one species of the subgenus *Leistus* Froehlig, 1799 and six species of the subgenus *Evanoleistus* Jedlička, 1967 (sensu Perrault 1980) are described as new At present, three species of the nominotypical subgenus and twenty six species of the subgenus *Evanoleistus* (Tschitschérine 1903, Dvořak 1994, Perrault 1994, Sciaky 1994, 1995, Farkač 1995) are known from Sichuan

We have used several indexes in the descriptions of the species, their list including their abbreviations used in the text, follows

antennal index	length of antennomere 5/length of antennomere 3 = IA
pronotal index	width/length of pronotum = IPw/l
pronotal index two	maximum width of pronotum/basal width of pronotum = IPm/b
elytral pronotal index	combined width of elytra/width of pronotum = IE/P
elytral index	length/width of elytra = IEl/w

Leistus (Leistus) cavazzutii sp. n.

(Figs 1, 13–14, 27)

DESCRIPTION (habitus of holotype as in Fig 27) Body length 8 8–9 4 (holotype 8 8) mm Piceous-brown Antennae from segment 5, mandibles, maxillary appendages and tarsi paler Mandibles long, acute Eyes prominent, large Gular setae situated on small transverse carina IA = 1 48–1 54

Pronotum (Fig 1) Large, transverse (IPw/l = 1 46–1 49, IPm/b = 1 84–1 97) Lateral margin evenly rounded Posterior angles obtuse Marginal bead flattly dilated from middle toward posterior angles Anterior margin of pronotum margined Basal area sparsely, but coarsely punctate Basal seta absent

Elytra widely oval, lateral bead narow. Shoulders not prominent, arcuate. Intervals almost flat, striae distinctive, grather coarsely punctate. Maximum width at middle. IE/P = 1.23–1.31, IEl/w = =1.54–1.58.

Aedeagus (Figs 13–14) similar to that of the European *L.* (*Leistus*) *piceus* Froehlig, 1799, but dilated distally, and with rather suddenly attenuate but obtuse apex.

AFFINITIES. *Leistus cavazzutii* sp. n. differs from *L.* (*Leistus*) *ludmilae* Dvořák, 1994 by the distinctly more transverse pronotum. Aedeagus of *L. ludmilae* is groove-like, parallelsided distally, and with obtuse apex. It differs from *L.* (*Leistus*) *cycloderus* Tschitschérine, 1903 by the shape of both the pronotum (Figs 1 and 8) and the aedeagus (Figs 13–14 and 27–28).

TYPE MATERIAL Holotype male, labelled. China, Sichuan, Mian Shan, 2700 m, VII–VIII 1995, lgt P F Cavazzuti In the collection of R. Sciaky (Milano). Paratypes: one male and one female, same data as holotype. In the collections of J. Farkač (Praha) and R Sciaky (Milano)

ETYMOLOGY. Patronymic, the species is named in honour of Pier Franco Cavazzuti (Pagno), the renowned *Carabus* specialist.

Leistus (*Evanoleistus*) *facchinii* sp. n.
(Figs 2, 15–16, 28)

DESCRIPTION (habitus of holotype in Fig. 28). Body length 8.5 mm (only holotype known). Head black, pronotum, elytra, femora and tibiae with brownish hue. Tarsi and maxillary appendages yellow-brown. Antennal segments yellow-brown, paler both proximally and basally. IA = 1.63. Eyes prominent. Gular setae situated on indistinct transverse carina.

Pronotum (Fig. 2) with lateral bead. Lateral margin evenly rounded, in front of posterior angles straight, but with faint sinuation. Posterior angles obtuse-angulate. Disc convex, smooth, shiny. Anterior margin, lateral bead and basal portion punctate. Posterior seta absent. IPw/l = 1.52, IPm/b = 2.09.

Elytra with rounded shoulders. Lateral bead slightly narrowed apicad. Lateral margins slightly rounded; elytra widest around middle. Strial punctation distinct. IE/P = 1.32, IEl/w = 1.68.

Aedeagus (Figs 15–16) curved in lateral view, with long and slender rounded apex.

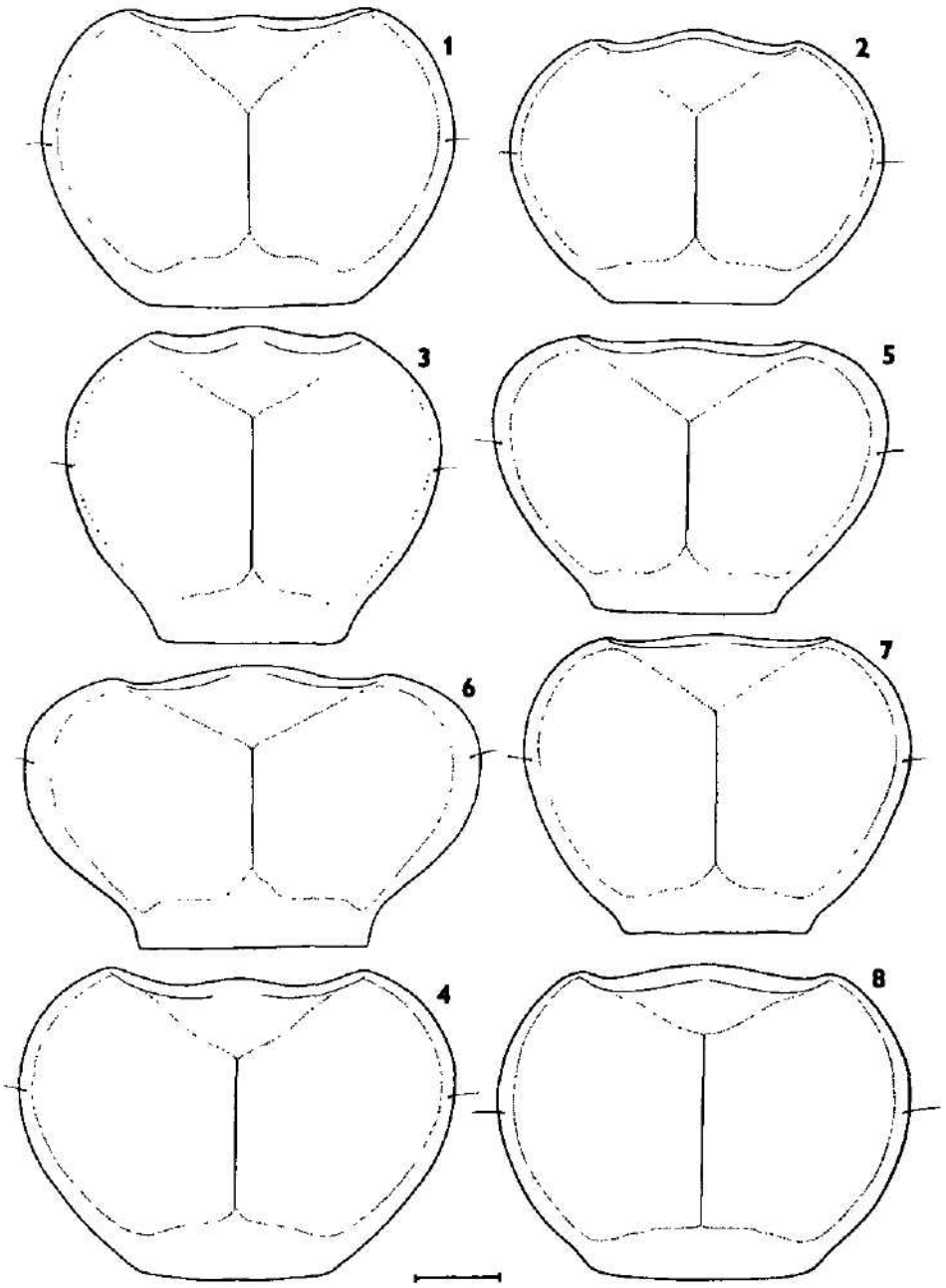
AFFINITIES. *L. facchinii* sp. n. differs from *L.* (*Evanoleistus*) *deuvei* Perrault, 1994 (from Huang Lang, Sichuan) of similar habitus, particularly by the entirely differently developed distal portion of the aedeagus (Figs 15–16 and Perrault 1994). It also differs from the habitually similar *L.* (*Evanoleistus*) *perraulti* Sciaky, 1993 (from Zhangla, Sichuan) by the differently shaped aedeagus (Figs 15–16 and Sciaky 1993). In both species the aedeagus has a considerably shorter and stouter apex, as compared to the slender and long apical portion of the aedeagus of the new species.

TYPE MATERIAL Holotype male, labelled China, Sichuan, Huang Long, VII 1996, [lgt] Moretto. In the collection of R Sciaky (Milano).

ETYMOLOGY. Patronymic, the species is named in honour of our friend, the renowned carabidologist Sergio Facchini (Milano).

Leistus (*Evanoleistus*) *haisishanicus* sp. n.
(Figs 3, 29)

DESCRIPTION (habitus of holotype in Fig. 29). Body length 9.7–10.2 (holotype 10.2) mm. Color dark brown, shiny. Tibiae, tarsi, antennae, mandibles and maxillary appendages paler. Antennae long, slender. Eyes not prominent. Gular setae situated on transverse carina. Legs very long. IA = 1.50–1.56.



Figs 1–8. Pronotum of: 1 – *Leistus* (*Leistus*) *cavazzutii* sp. n.; 2 – *L.* (*Evanoleistus*) *facchinii* sp. n.; 3 – *L.* (*E.*) *haisishanicus* sp. n.; 4 – *L.* (*E.*) *mirosiavae* sp. n.; 5 – *L.* (*E.*) *wolong* sp. n.; 6 – *L.* (*E.*) *wrasei* sp. n.; 7 – *L.* (*E.*) *zamotajlovi* sp. n.; 8 – *L.* (*Leistus*) *cycloderus* Tschitschérine (holotype). Scale 1 mm.

Pronotum (Fig. 3) very narrow (lPw/l = 1.22–1.27), with shiny, convex disc, lateral margin slightly sinuate in front of posterior angles. Posterior angles obtusely angulate. Lateral bead narrow. Anterior margin, basal area and lateral bead markedly, coarsely punctate. Basal seta absent. lPm/b = =1.99–2.07.

Elytra oval, stout with slightly prominent shoulders, maximum width middle. Elytral intervals flat, striae markedly punctate. lE/P = 1.52–1.58, lEl/w = 1.50–1.62.

Male unknown.

Affinities. *Leistus haisishanicus* sp. n. differs from the only other species of similar habitus, *Leistus* (*Evanoleistus*) *cylindricus* Sciaky, 1994 (from Zhangla) by the presence of the lateral bead on pronotum (absent in *L. cylindricus*) and by the more distinctive punctation of the elytra (Fig. 25 and Sciaky 1994).

Type material. Holotype, female, labelled: China, Sichuan, Kangding distr., SE slopes of Mt Haisishan (Varala), 4100–4600 m, 21 vii 1996, lgt. A. Zamotajlov, A. Miroshnikov & D. Fedorenko. In the collection of Alexander S. Zamotajlov (Krasnodar). Paratypes: two females, same data as holotype. In the collections of J. Farkač (Praha) and A. S. Zamotajlov (Krasnodar).

Etymology. The specific name is derived from the name of the mountain range Haisishan, the type locality.

Leistus (*Evanoleistus*) *miroslavae* sp. n.
(Figs 4, 17–18, 30)

Description (habitus of holotype as in Fig. 30). Body length 8.7–9.2 (holotype 8.8) mm. Color dark brown, tarsi, antennae, mandibles and maxillary appendages paler. Eyes prominent. Gular setae situated on transverse carina. Mandibles relativelly short, outer lateral margin anly slightly sinuate. lA = 1.54–1.66.

Pronotum (Fig. 4). Lateral margin rounded, straighter from middle toward base than toward apical margin, maximum width before middle. Posterior angles obtusely angulate. Lateral bead slightly dilated toward basal depressions. Punctation of anterior margin and base indistinct, punctation of lateral bead very fine. Basal seta absent.

lPw/l = 1.48–1.53, lPm/b = 2.00–2.11.

Elytra. Rounded but with appreciable shoulders. Lateral margins almost parallel in middle third. Intervals flat, strial punctation indistinct. lE/P = 1.21–1.27, lEl/w = 1.56–1.61.

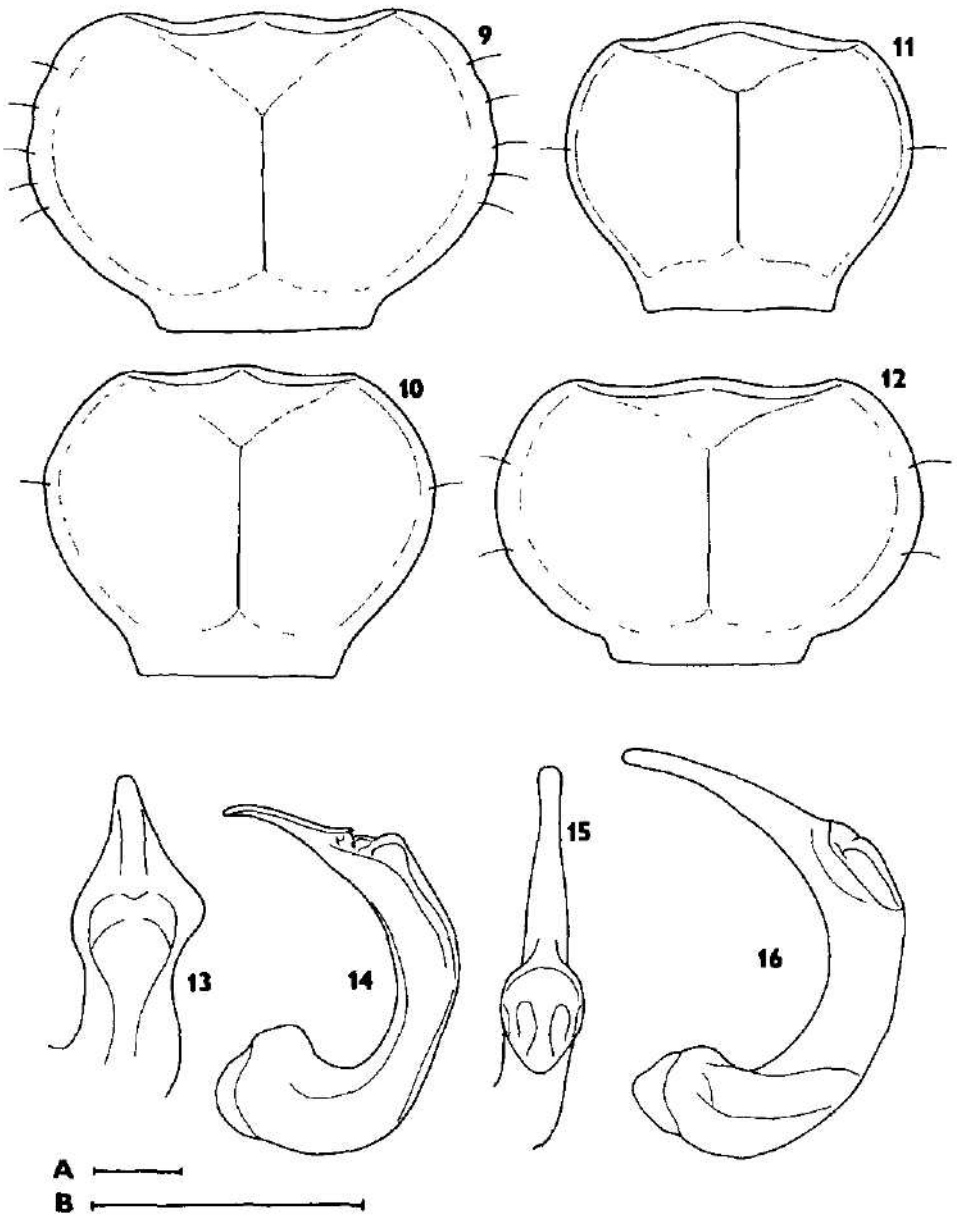
Aedeagus (Figs 17–18). Distal portion of aedeagus groove-like, apex obtuse.

Affinities. *Leistus miroslavae* sp. n. differs from *L.* (*Evanoleistus*) *haeckeli* Farkač, 1995 and *L.* (*Evanoleistus*) *sciakyi* Farkač, 1995 (both Gongga Shan massive, Sichuan) both with similar aedeagus, by the different shape of pronotum (Fig. 4 and Farkač 1995). It differs from *L.* (*Evanoleistus*) *vignai* Sciaky, 1995 (Sichuan: between Jiuzhaigou and Songpan) by the more parallel-sided elytra, and by the different shape of the pronotum and aedeagus (Figs 4, 17–18, 30 and Sciaky 1995).

Type material. Holotype: male, labelled: CH, N-Sichuan (Barkam), valley SW of Barkam, 31 53N 102 12E, 3000–3800 m, 22 vii 1995, lgt. M. Janata. In the collection of J. Farkač (Praha). Paratypes: three males, same data as holotype. In the collections of J. Farkač (Praha) and Miroslav Janata (Praha).

Etymology. Patronymic, named in honour of collector's daughter.

Collection circumstances. All specimens were taken in mixed/ coniferous forest.



Figs 9–16 Pronotum of: 9 – *L. (Evanoleistus) crenifer* Tschitschérine, 1903 (holotype), 10 – *Leistus (E.) gracilentus* Tschitschérine (holotype), 11 – *L. (E.) gracilimus* Tschitschérine (holotype), 12 – *L. (E.) nubicola* Tschitschérine (holotype); Aedeagus of holotypes in dorsal and lateral view of 13, 14 – *L. (Leistus) cavazzuti* sp. n., 15, 16 – *L. (Evanoleistus) facchinii* sp. n. Scale 1 mm (A: Figs 9–12, B: Figs 13–16).

Leistus (*Evanoleistus*) *wolong* sp. n.
(Figs 5, 19–20, 31)

DESCRIPTION (habitus of holotype in Fig. 31). Body length 8.5–9.3 (holotype 9.0) mm. Color piceous-black with paler tarsi, mandibles, antennae and maxillary appendages. Eyes developed in usual way. Gular setae situated on transverse carina. IA = 1.47–1.60.

Pronotum (Fig. 5) heart-shaped (IPm/b = 2.00–2.13). Lateral bead wider and flat, narrowed toward posterior angles. Disc convex, basal depression coarsely punctate. Posterior angles obtuse-angulate. IPw/l = 1.42–1.57.

Elytra. Convex, lateral margins sub-parallel. Shoulders prominent. Strial punctation distinctive, intervals flat. IE/P = 1.35–1.39, IEl/w = 1.60–1.64.

Aedeagus (Figs 19–20). Distal portion curved, with obtuse apex.

AFFINITIES. *Leistus wolong* sp. n. differs from *L. gansuensis* Sciaky, 1995 (Gansu: between Xiahe and Heznojhen) of similar habitus by the narrower pronotum (Fig. 5 and Sciaky 1995), by the more prominent elytral shoulders, and by the longer, before the end curved, apex of the aedeagus (Figs 19–20 and Sciaky 1995).

TYPE MATERIAL. Holotype: male, labelled: Sichuan, Wolong, 4400 m. In the collection of J. Farkač (Praha). Paratypes: one female, same data as holotype and two males, labelled: China, Sichuan, Wolong–Rilong, 4200 m, VII 1996. In the collections of Thiery Deuve (Muséum national d'Histoire naturelle, Paris), R. Sciaky (Milano) and S. Facchini (Milano).

ETYMOLOGY. The specific name is derived from the name of the village Wolong, in the vicinity of which the new species was found.

Leistus (*Evanoleistus*) *wrasei* sp. n.
(Figs 6, 21–22, 32)

DESCRIPTION (habitus of holotype in Fig. 32). Body length 9.1–9.6 (holotype 9.3) mm. Black. Antennae, mandibles, maxillary appendages, legs and lateral margins of lateral bead of pronotum brownish. Mandibles long, acute. Eyes prominent, large. Gular setae situated on fine transversal carina. IA = 1.25–1.45.

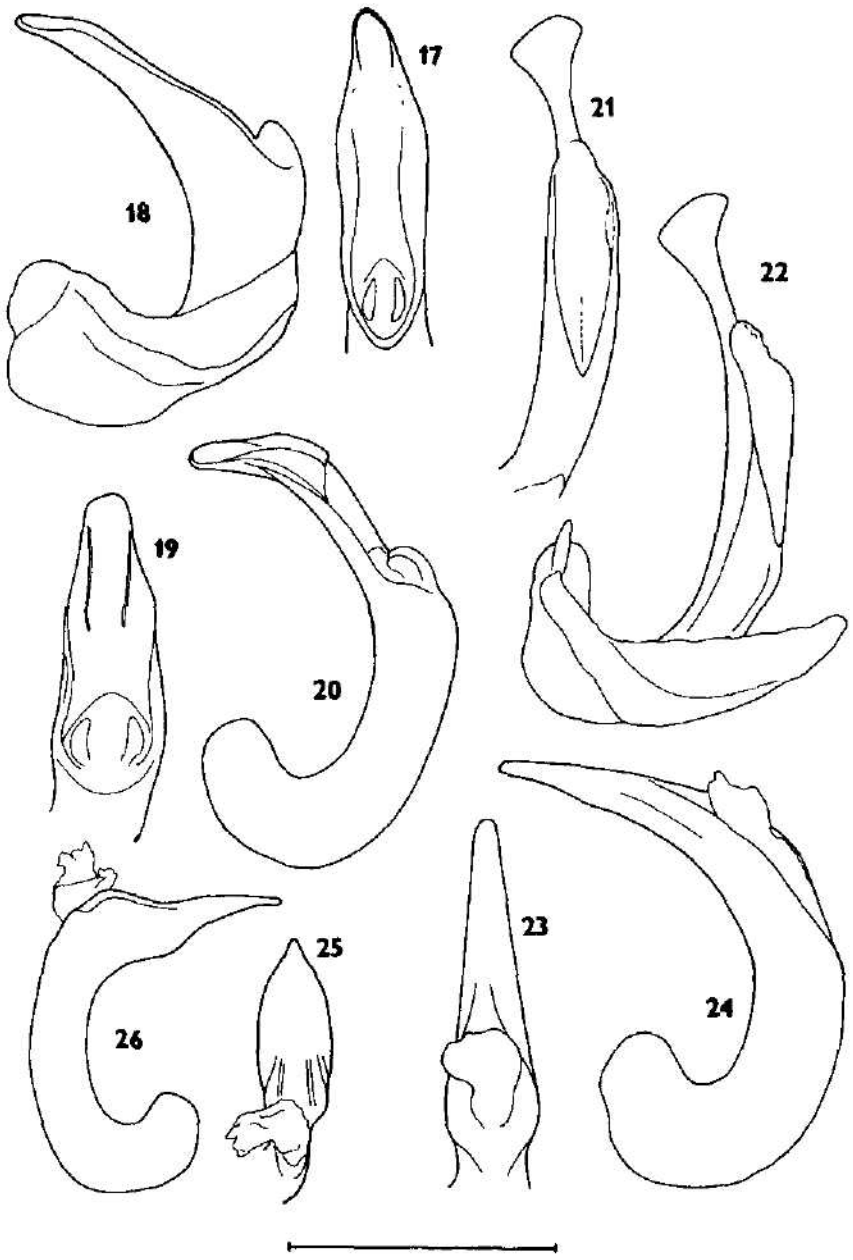
Pronotum (Fig. 6) large, transverse (IPw/l = 1.54–1.61, IPm/b = 1.91–2.00). Lateral margin sinuate before hind angles, hind angles almost rectangular. Lateral bead of pronotum wide, flat, narrowed toward hind corners. Basal depression sharply delimited from pronotal disc, sparsely but coarsely punctate. Basal seta absent.

Elytra parallel-sided, humeri appreciable, rounded. Intervals flat, striae coarsely punctate. Four or five setiferous punctures in third interval. IE/P = 1.15–1.28, IEl/w = 1.60–1.80.

Aedeagus (Figs 21–22) attenuate distally past ostium and then assymetrically securiform, rotated to left.

AFFINITIES. *Leistus wrasei* sp. n. resembles habitually *L.* (*E.*) *yunnanus* Bänninger, 1925 (from Yunnan) and *L.* (*E.*) *brancuccii* Farkač, 1995 (from Yunnan and Guizhou). It differs from *L. yunnanus* by the wider pronotum and narrower elytra, and from *L. brancuccii* by the sinuation of the lateral margin of the pronotum (Fig. 6, Perrault 1985 and Farkač 1995). It differs from both species by the different shape of the distal portion of the aedeagus (Figs 21–22, Perrault 1985 and Farkač 1995).

TYPE MATERIAL. Holotype: male, labelled: China (W. Sichuan), 29 36N 102 04E, Daxue Shan, Hailuogou Glacier Park (Gongga Shan), Camp 1, 2100 m, 27./28./31. V. [19]97, Wrase [leg.]. Paratypes: three males and three females, same data as holotype, four males and three females, labelled: China: Sichuan, Daxue Shan, Gongga Shan Mt., Hailougou Glacier Park, 102 04E 29 36N, river valley ca. 1km above Camp 1, 2100 m, 28./31.V.1997, leg. A. Putz. In the collections of J. Farkač (Praha), D. W. Wrase (Berlin) and A. Pütz (Eisenhüttenstadt).



Figs 17–26. Aedeagus of holotypes in dorsal and lateral view of 17, 18 – *L. (Evanoleistus) miroslavae* sp. n.; 19, 20 – *L. (E.) wolong* sp. n.; 21, 22 – *L. (E.) wraseri* sp. n.; 23, 24 – *L. (E.) zamotajlovi* sp. n. 25, 26 – *L. (E.) cycloderus* Tschitschérine. Scale 1 mm.

ETYMOLOGY. Patronymic, the species is named in honour of our friend, the renowned carabidologist and collector of the new species David W. Wrase (Berlin).

Leistus (Evanoleistus) zamotajlovi sp. n.
(Figs 7, 23–24, 33)

DESCRIPTION (habitus of holotype in Fig. 33). Body length 9.7–9.9 (holotype 9.7) mm. Color dark piceous-brown, mandibles, maxillary appendages, tarsi and antennae from segment 5 paler, yellowish. Antennal segments 1–4 dark with paler distal end. Eyes normal. Gular setae situated on transverse carina. IA = 1.51–1.56.

Pronotum (Fig. 7) heart-shaped (IPm/b = 2.00–2.11). Disc convex, with distinct medial line. Lateral bead dilated toward posterior angles. Basal area punctate, basal depressions on posterior angles distinct. Lateral margins sinuate in front of posterior angles, basal angles therefore almost rectangular. Basal seta absent. IPw/l = 1.25–1.42.

Elytra Elongate oval, with maximum width behind middle. No apparent shoulders, lateral bead narrow. Strial punctation fine, intervals almost flat. IE/P = 1.15–1.38, IEl/w = 1.64–1.75.

Aedeagus (Fig. 23–24). Distal portion long, tapering toward obtuse apex.

AFFINITIES. *L. zamotajlovi* sp. n. differs from *L. (Evanoleistus) saueri* Sciaky, 1993 (from the same locality) by the slenderer habitus, by the different aedeagus (Figs 23–24 and Sciaky 1993), as well as by the differently shaped pronotum (Fig. 7 and Sciaky 1993).

TYPE MATERIAL Holotype: male, labelled: China, Sichuan, Kangding distr., Lake Xierenhai (Mugelçuo) vic., 3900 m, 23.–24.VII 1996, lgt. A. Zamotajlov, A. Miroshnikov & D. Fedorenko. In the collection of Alexander S. Zamotajlov (Krasnodar). Paratypes: Two males, same data as holotype. In the collections of J. Farkač (Praha), and A. S. Zamotajlov (Krasnodar).

ETYMOLOGY Patronymic, named in honour of Alexander S. Zamotajlov (Russian Academy of Sciences, Krasnodar), the collector of this new species.

Lesistus (Leistus) ludmilae Dvořák, 1994

Leistus (Leistus) ludmilae Dvořák, 1994: 6

MATERIAL EXAMINED One female specimen, labelled: China, W Sichuan, 31.55N, 98.53E, Chola Shan mts., 19.VII 1997, road Dege – Manganggo, 40 km E of Dege, cca 4200 m, picea forest, M. Trýzna & O. Šafránek lgt.

The species was until now known only from the two specimens of the original series. The additional specimen was compared with the holotype in the collection of M. Dvořák (Praha).

Leistus (Evanoleistus) haeckeli Farkač, 1995

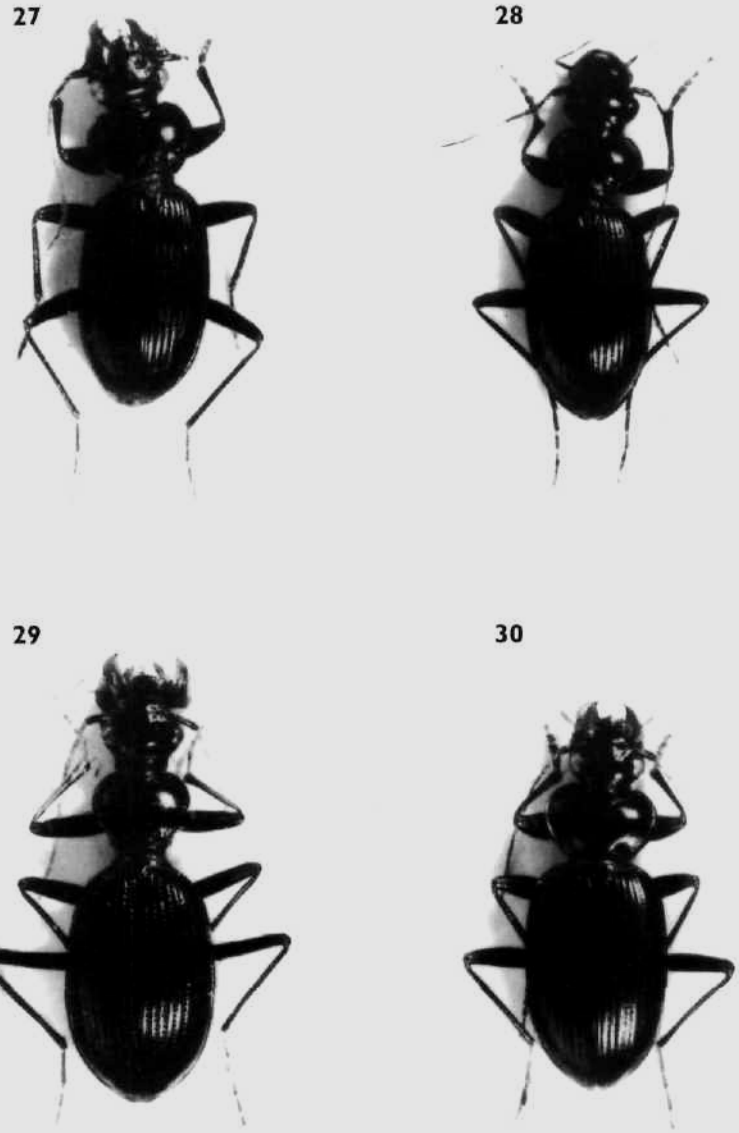
Leistus (Evanoleistus) haeckeli Farkač, 1995: 152–153

MATERIAL EXAMINED Four specimens, labelled: China, Sichuan, Gongga Shan, Hailuogou, above Camp 3, 29.35N 102.00E, 3200 m, 7.VII 1996, lgt. J. Farkač, P. Kabátek and A. Smetana.

The species was previously known only from the specimens of the original series (Farkač 1995) from the same locality. The additional specimens were compared with the holotype in the collection of J. Farkač (Praha).

Leistus (Evanoleistus) kangdingensis Farkač, 1995

Leistus (Evanoleistus) kangdingensis Farkač, 1995: 154



Figs 27–30. Habitus of holotypes of: 27 – *Leistus* (*Leistus*) *cavazzutii* sp. n.; 28 – *L.* (*Evanoleistus*) *facchinii* sp. n.; 29 – *L.* (*E.*) *haisishanicus* sp. n. ; 30 – *L.* (*E.*) *miroslavae* sp. n.

Figs 31–33. Habitus of holotypes of: 31 – *Leistus* (*E.*) *wolong* sp. n.; 32 – *L.* (*E.*) *wrasei* sp. n.; 33 – *L.* (*E.*) *zamotajlovi* sp. n.

MATERIAL EXAMINED Two specimens, labelled China, Sichuan, Pass ca 30km W Kangding, 4000–4200 m, 12 vi 1995, lgt [W.] Heinz

Only the original series of specimens (Sichuan 16 and 30 km W of Kangding) of this species was known until now (Farkač 1995) The additional specimens were compared with the holotype in the collection of J Farkač (Praha)

Leistus (Evanoleistus) pseudocrenifer Sciaky, 1995

Leistus (Evanoleistus) pseudocrenifer Sciaky, 1995 293

MATERIAL EXAMINED One male specimen, labeled W Sichuan, Aba co , Barkam, 3500m, vi 1994, M Hackel leg

Only the original series of specimens (N Sichuan Jiuzhaigou and Barkam S-environs) of this species was known until now (Sciaky, 1995) The additional specimen were compared with the paratype in the collection of J.Farkač (Praha)

Leistus (Evanoleistus) saueri Sciaky, 1994

Leistus (Evanoleistus) saueri Sciaky, 1994 208–209

MATERIAL EXAMINED Four specimens, labelled China, Sichuan, Umg Kangding, See Mugeçuo, 3600–3800 m, 11 – 13 vi 1995, lgt [W.] Heinz

The species was known until now only from the specimens of the original series (W Sichuan Mugezo Lake) (Sciaky 1994)

Leistus (Evanoleistus) shuamaluko Farkač, 1995

Leistus (Evanoleistus) shuamaluko Farkač, 1995 156–158

MATERIAL EXAMINED One specimen, labelled CH, Sichuan (Hongyuan), wall 10 km SE Sanggarpar (alpine meadow / scree), 32 18N 102 35E, 4200m, 19 vii 1995, lgt K & B Březina

The species was previously known only from the holotype (Sichuan Shuamaluko) (Farkač 1995) The additional specimen was compared with the holotype in the collection of J Farkač (Praha)

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REFERENCES

DVOŘAK M 1994 Einige neue Leistus Arten (Coleoptera, Carabidae, Nebriini) *Annot Zool Bot* **215** 1–11

FARKAČ J 1995 Sixteen new species of Leistus from Asia (Coleoptera Carabidae Nebriini) *Acta Soc Zool Bohem* **59** 145–163

PERRAULT G G 1980 Le genre Leistus Froehlig (Coleoptera, Carabidae) II Division en sous genres *Bull Soc Linn Lyon* **49** 456–463

PERRAULT G.-G. 1985. Le genre Leistus Frochlig (Coleoptera – Carabidae – Nebriini). VI. – Le sous-genre Evanoleistus Jedlička (1). *Bull. Soc. Linn. Lyon* **54**: 13–24.
PERRAULT G.-G. 1994. Le genre Leistus Frochlig (Coleoptera, Carabidae). XVII. Les Leistus de l'interieur de la Chine (Tschitscherine, 1903). *Bull. Mens. Soc. Linn. Lyon* **63**: 165–172.
SCIAKY R. 1994. Seven new species of Leistus from China (Coleoptera Carabidae Nebriinae). *Acta Soc. Zool. Bohem.* **57**(1993): 203–210.
SCIAKY R. 1995. Four new species of Leistus from China (Coleoptera, Carabidae, Nebriinae). *Fragm. Entomol. Roma* **26**: 293–303.
TSCHITSCHÉRINE T. 1903. Les Leistus de l'interieur de la Chine. *Horae Soc. Entomol. Ross.* **36**: 22–37.
WU C.-H. F. 1937. *Catalogus insectorum sinensium* (*Catalogue of chinese insects*). *III*. Peiping: The Fan Memorial Institute of Biology, 256 pp.

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Emmonsiosis of small mammals (Rodentia, Insectivora) in the Pálava Biosphere Reserve of the UNESCO

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Abstract. Adiaspores of the fungus *Emmonsia parva* var *crescens* were detected in the lungs of 288 animals (11 8% of *Sorex araneus*, 1 of 5 *Crocidura suaveolens*, 19 6% of *Microtus arvalis*, 1 of 3 *M subterraneus*, 36 1% of *Clethrionomys glareolus*, 23 3% of *Apodemus flavicollis* and 19 8% of *A sylvaticus*) out of 1197 small mammals (Soricidae, Arvicolidae, Muridae) of 10 species examined in the Palava Biosphere Reserve South Moravia, Czech Republic The mammals were caught in May and October, 1989–1993 The overall prevalence of emmonsiosis (adiasporomycosis) was 24 3% in rodents (42 3% in adults) and 12 5% in insectivores (25 0% in adults) *Emmonsia* infection was significantly more frequent in adult (42 0%) than in juvenile (13 3%) mammals and also varied according to habitat

Rodentia, Insectivora, Emmonsia, adiaspores, mycosis, disease

INTRODUCTION

Emmonsiosis (adiasporomycosis) is a pulmonary infection of mammals caused by fungi of the genus *Emmonsia*, most often *E parva* var *crescens* (Emmons et Jellison, 1960) van Oorschot 1980 (Emmons & Jellison 1960, Dvořák et al 1973) The infection is widespread among small mammals in South Moravia, Czech Republic (Hubálek et al 1991), but only a limited sample of mammals (n=110) has been tested so far in the area of the Pavlovské vrchy Hills The present investigation has followed and supplemented a long-term ecological and faunal study of small mammalian communities in that important bioreserve of the UNESCO (Gaisler et al 1996)

MATERIAL AND METHODS

The Palava Biosphere Reserve (83 km^2) is situated at the town Mikulov in South Moravia, on the border between the Czech Republic and Austria The climate is warm and moderately dry For a description of the area and further details, see Gaisler et al (1996)

Small mammals were caught in snap traps and live traps during May and October (a few in August) in the years 1989 to 1993 The traps were laid along 12 standard lines and in one quadrat (Gaisler et al l c, Fig 1) Captured animals were determined, sexed and aged For the purpose of this study, sexually active animals and those in sexual regression were considered as adults while all other animals as juveniles

The whole lungs of mammals were placed in 2% KOH overnight, and then examined microscopically, adiaspores of *Emmonsia* were counted and measured Differences in the prevalence of infection were evaluated by the chi-square test

Tab. 1 *Emmonsia* infection according to the host species

	All animals			Adults only		
	n[1]	inf[2]	%	n[1]	inf[2]	%
Sorex araneus Linnaeus, 1766	17	2	11.8	6	1	16 7
S minutus Linnaeus, 1766	1	–	–	–	–	–
Crocidura suaveolens (Pallas, 1821)	5	1	(20)	2	1	(50)
Talpa europaea Linnaeus, 1758	1	–	–	–	–	–
Microtus arvalis (Pallas, 1779)	199	39	19.6	72	20	27.8
M subterraneus (de Sélys-Longchamps, 1836)	3	1	(33)	1	–	–
Clethrionomys glareolus (Schreber, 1780)	233	84	36.1	90	51	56 7
Apodemus sylvaticus (Linnaeus, 1758)	298	59	19 8	81	39	48 1
A flavicollis (Melchior, 1834)	437	102	23.3	196	76	38 8
Micromys minutus (Pallas, 1771)	3	–	–	–	–	–
Total	1197	288	24 1	448	188	42 0

[1]no. of animals examined
[2]no of animals infected

RESULTS

A total of 288 animals out of 1197 examined (24.1%) and 188 of 448 adult mammals (42.0%) were infected (Tab. 1). All adiaspores were typical of *Emmonsia parva* var. *crescens*, with the mean diameter >70 μm. Two insectivore and five rodent species out of 10 mammalian species examined were infected: *Sorex araneus*, *Crocidura suaveolens*, *Microtus arvalis*, *M. subterraneus*, *Clethrionomys glareolus*, *Apodemus flavicollis* and *A sylvaticus*. The overall prevalence of emmonsiosis was 24.3% in rodents (42.3% in adults) and 12.5% in insectivores (25.0% in adults). The prevalence rate was significantly higher in the genus *Clethrionomys* (36.1%) than in *Apodemus* (21.9%) or *Microtus* (19.8%); corresponding rates for the adults were 56.7%, 41.5% and 27.4%, respectively. The higher prevalence rate of emmonsiosis in *Clethrionomys* was significant for animals of all age groups (χ^2=16.62; P<0.001) as well as for adults (χ^2=8.27; P<0.02).

Emmonsiosis was uniformly distributed between male and female mammals (Tab. 2: χ^2=1.54 and P>0.20 for all age groups; χ^2=0.14 and P>0.70 for adults) but it was significantly more frequent in adults (42.0%) than in juveniles (13.3%; Tab. 2: χ^2=95.63; P<0.001) and it also varied according to habitat (Tab. 3). E.g., the mammals caught on shrubby foothill ecotone of the main limestone ridge were significantly more often infected than those from the other habitats (χ^2=16.025; P<0.02). The lowest infection rate of mammals was found in the sample from a deciduous mixed forest affected by deer breeding (the Milovice game preserve).

Tab 2 *Emmonsia* infection according to the host age and sex

	n	inf	%
Adults	448	188	42.0
Juveniles	750	100	13.3
Males (all age groups)	587	130	22.1
Females (all age groups)	608	156	25.7
Adult males	*199*	*81*	*40 7*
Adult females	249	107	43 0

Tab. 3. *Emmonsia* infection according to the host habitat

	All animals			Adults only		
	n	inf	%	n	inf	%
Deciduous forests of the main limestone ridge	321	82	25 5	142	61	43.0
Grassland on limestone soil	77	20	26 0	33	11	33 3
Karren fields	150	36	24 0	59	28	47 5
Shrubs at the foothills	178	62	34 8	57	34	59 6
Deciduous forests affected by deer breeding	214	34	15.9	72	21	29.2
Floodplain forest	158	32	20.3	54	22	40.7
Floodplain meadow	99	22	22.2	31	11	35.5

The prevalence of emmonsiosis was higher in May (32.0%) than in October (22.0%; Tab. 4: χ^2=7.64, P<0.01). This was due to relatively more juveniles obtained in the October (72.5%) than in the May (24.9%) sample. In adult mammals, the prevalence rate was identical for the two months (χ^2=0.001, P>0.99).

The mean intensity of *Emmonsia* infection was 175 adiaspores per infected animal (185 in adults), with a maximum of 6045 adiaspores (*Apodemus sylvaticus*) and a minimum of only one adiaspore (53 cases). The mean infection intensity values varied among the rodent species: they were higher in *A. sylvaticus* (370 adiaspores per infected animal), *Microtus arvalis* (191) and *Apodemus flavicollis* (128) than in *Clethrionomys glareolus* (93). Re-infection (adiaspores of two distinct size classes present in the lungs of an animal) was found in 10.1% of infected mammals; the re-infection rate also fluctuated for individual species: *Sorex araneus* 1/2, *Microtes arvalis* 12.8%, *Clethrionomys glareolus* 13 1%, *Apodemus sylvaticus* 11.9% and *Apodemus flavicollis* 4.9%.

The mean diameter of adiaspores in mammals varied between 31 and 511 μm, with an arithmetic mean of 217 μm. Average adiaspore sizes were 285 μm in *Sorex araneus*, 141 μm in *Crocidura suaveolens*, 173 μm in *Microtus arvalis*, 97 μm in *Microtus subterraneus*, 331 μm in *Clethrionomys glareolus*, 165 μm in *Apodemus flavicollis* and 173 μm in *Apodemus sylvaticus*.

DISCUSSION

The overall prevalence rate of rodent emmonsiosis in seven different habitats of the Pálava Biosphere Reserve was 24.3%, and 42.3% in adults. It was higher than average data from S. Moravia, i.e. 16.2% and 20.4%, respectively (Hubálek et al. 1991). Emmonsiosis was significantly more frequent in *Clethrionomys* than in the two other rodent genera, *Apodemus* and *Microtus*. *Sorex araneus*, *Crocidura suaveolens* and *Microtus subterraneus* are new host species of *Emmonsia parva* var. *crescens* in S. Moravia. The present results confirm previous studies (Prokopič 1971, Dvořák et al. 1973, Hubálek et al. 1991, 1993) that the host's sex does not play a role in the distribution of emmonsiosis, while the pronounced age effect reflects the prolonged exposure of the host to the fungal agent in the environment. The distribution of emmonsiosis was relatively homogeneous among habitats of the Pálava Biosphere Reserve, with two significant exceptions: the shrubby

Tab. 4. *Emmonsia* infection according to season

	All animals			Adults only		
	n	inf	%	n	inf	%
May	225	72	32 0	169	71	42 0
October	955	210	22 0	263	111	42 2

foothill ecotone with a higher prevalence, and the deciduous forest affected by deer (*Cervus elaphus, Dama dama*) breeding at Milovice with a lower prevalence of emmonsiosis. Interestingly, rather high rodent emmonsiosis rates were detected in the floodplain-forest ecosystem at Bulhary. This is, however, in accord with another study from S. Moravia (Hubálek et al. 1993). The mean intensity of infection was higher in the genus *Apodemus* than in *Clethrionomys*; conversely, the mean diameter of adiaspores was greater in *Clethrionomys* than in *Apodemus*. Very similar results were obtained in the previous study (Hubálek et al. 1991). Also the re-infection rate of rodents was nearly identical in both studies: 9.8% vs. 11.6%.

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REFERENCES

Dvořak J., Otčenášek M. & Rosicky B. 1973: Adiaspiromycosis caused by Emmonsia crescens, Emmons et Jellison 1960. *Studie ČSAV* **14**: 1–120.

Emmons C. W. & Jellison W. L. 1960: Emmonsia crescens sp. n. and adiaspiromycosis (haplomycosis) in mammals. *Ann. N. Y. Acad. Sci.* **89**: 91–101.

Gaisler J., Zukal J., Nesvadbová J., Chytil J. & Obuch J. 1996: Species diversity and relative abundance of small mammals (Insectivora, Chiroptera, Rodentia) in the Pálava Biosphere Reserve of UNESCO. *Acta Soc. Zool. Bohem.* **60**: 13–23.

Hubálek Z., Zejda J., Nesvadbová J. & Rychnovsky B. 1991: Adiasporomycosis – a widespread disease of rodents in southern Moravia, Czechoslovakia. *Folia Zool.* **40**: 107–116.

Hubálek Z., Zejda J., Svobodová Š. & Kučera J. 1993: Seasonality of rodent adiasporomycosis in a lowland forest. *J. Med. Vet. Mycol.* **31**: 359–366.

Prokopič J. 1971: The distribution of adiaspiromycosis in small mammals of the Czech Socialist Republic. *Folia Parasitol.* **18**: 323–327.

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Larval taxonomy, development and diet of *Amara* (*Amara*) *famelica*, *A.* (*A.*) *littorea* and *A.* (*A.*) *proxima* (Coleoptera: Carabidae: Amarina)

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Abstract. Three larval instars of *Amara* (*Amara*) *famelica* Zimmermann, 1832, *A* (*A*.) *littorea* C G Thomson, 1857 and *A* (*A*.) *proxima* Putzeys, 1866 are described and illustrated Differential diagnosis of the nominotypical subgenus *Amara* Bonelli, 1810, based on the larval characters, is given Data on the developmental time and the breeding type of all three reared species are mentioned All three species laid eggs on the mixed vegetable (oat flakes) and insect (*Tenebrio* larvae) diet, for *A littorea* the offered diet was of the lowest value Larvae and pupae of *A famelica* and *A proxima* were able to survive on a pure insect diet, *A famelica* larvae and pupae also on a pure vegetable and a mixed vegetable+insect diet

Larval taxonomy, breeding type, developmental time, larval diet, Coleoptera, Carabidae, *Amara*, Palaearctic Region

INTRODUCTION

Out of about 80 species of the nominotypical subgenus *Amara* Bonelli, 1810, at least some larval characters are mentioned in 15 species (Arndt 1991, Bílý 1972, Burakowski 1967, Desender 1988, Desender et all 1986, Habu & Sadanaga 1963, Luff 1993, Thompson 1979). Nevertheless, not even one third of these larval descriptions includes all necessary data on morphology and chaetotaxy, and illustrations of the distinguishing characters. The aim of this paper is. (1) to give the taxonomic diagnoses of further three species, contributing to the determination of differential diagnosis of the subgenus in the larval stage, and (2) to provide bionomic data concerning the development and the breeding type of these relatively rarely occurring species.

MATERIAL AND METHODS

Three larval instars of *Amara* (*Amara*) *famelica* (14 L_1, 12 L_2, 19 L_3), of *A* (*A*.) *littorea* (5 L_1, 2 L_2, 5 L_3) and of *A* (*A*.) *proxima* (14 L_1, 12 L_2, 11 L_3) are reared ex ovo, according to the technique described by Hůrka (1996) The parental pairs are found as follows *A* (*A*.) *famelica* – Bohemia occ , Slavkovsky les Mts , Krasno (code of mapping square 5842*), peet-bog, 780 m, 3 v 1990, J Hejkal leg , *A* (*A*.) *littorea* – Bohemia centr , Praha-Ruzyně (5951), field, 24 iv 1995, A Honěk leg , Bomemia centr , Praha-Radotín, Cikánka env (6051), fallow, 2 iv 1997, K Hůrka leg , *A* (*A*.) *proxima* – Slovakia mer , Plašťovce (7879), 17 iv 1995, J Hejkal leg

For comparative purpouse larvae of following taxa have been studied *Amara* (*Amara*) *aenea* (De Geer, 1774), *A* (*A*.) *communis* (Panzer, 1797), *A* (*A*.) *convexior* Stephens, 1828, *A* (*A*.) *curta* Dejean, 1828, *A* (*A*.) *eurynota* (Panzer, 1797), *A* (*A*.) *makolskii* Roubal, 1923, *A* (*A*.) *pulpani* Kult, 1949, *A* (*A*.) *spreta* Dejean, 1831, *A* (*Amarocelia*) *erratica* (Duftschmid, 1812), 6 species of the subgenus *Celia* Zimmermann, 1832, *A* (*Paracelia*) *quenseli quenseli* (Schonherr, 1806), *A* (*Percosia*) *equestris equestris* (Duftschmid, 1812), 5 species of the subgenus *Bradytus* Stephens, 1828 and 3 species of the subgenus *Curtonotus* Stephens, 1828

All larvae are deposited in the Collectio Hůrka of the Charles University Praha, Department of Zoology The notation of setae and pores follows the papers by Bousquet & Goulet (1984) and Bousquet (1985)

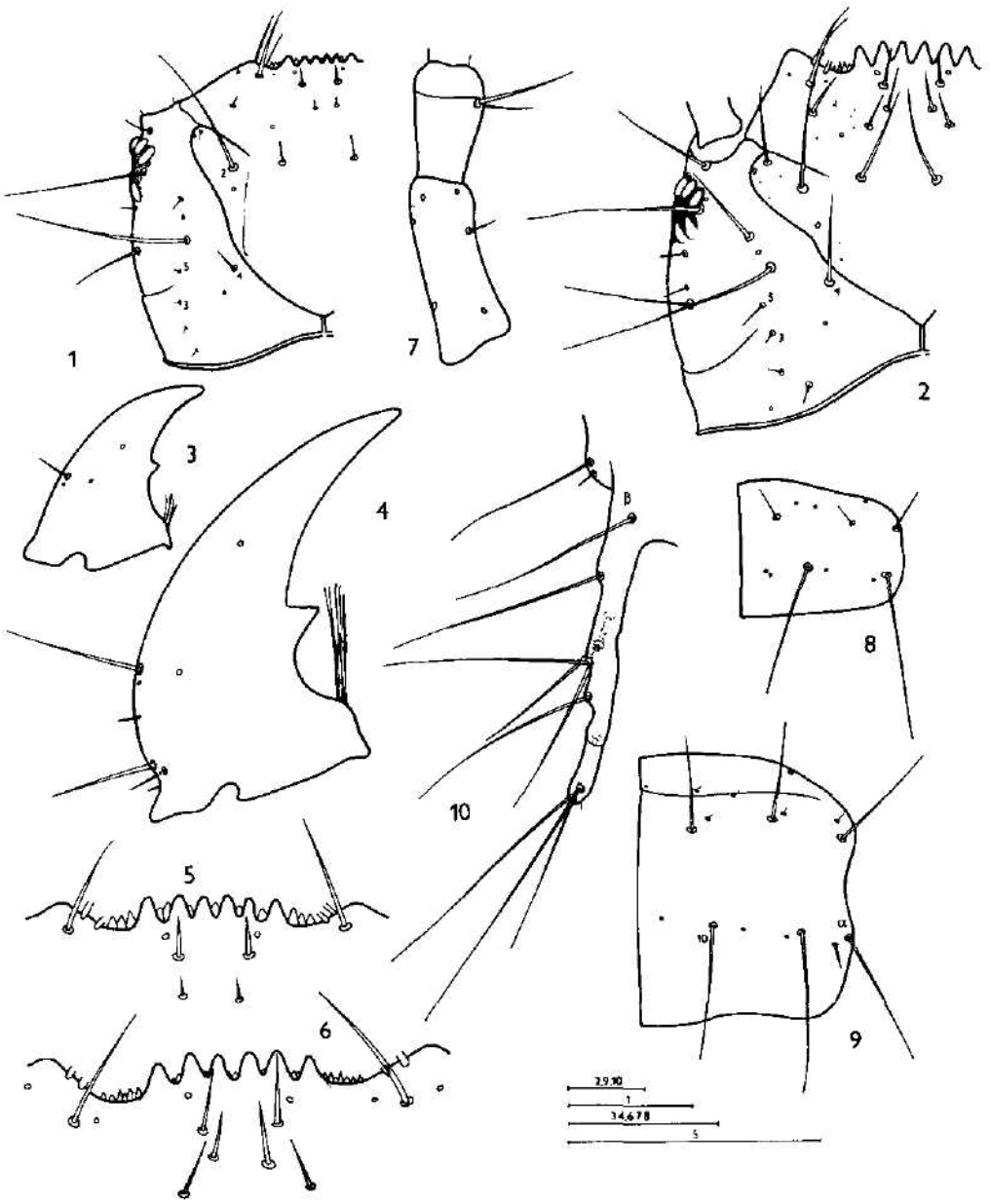
*) for details see Buchar (1982)

Amara (*Amara*) *famelica* Zimmermann, 1832
(Figs 1–10)

COLOUR. Head, thoracic and abdominal terga pale rusty brown, head and pronotum darkened.
THIRD INSTAR. Head: cephalic capsule transverse (index width/length = 1.50–1.60), sides slightly convex; cervical grooves deep, reaching dorsally space between PA_3 and PA_5 and almost reaching PA_{15} ventrally; coronal suture as long as two thirds of antennomere IV; nasale with 6 large teeth, the two and two inner teeth slightly less spaced (Fig. 6); mandibles with one longer and three shorter secondary setae (Fig. 4); antennomere I with one small secondary seta, antennomere II with obligatory two (rarely one) secondary setae (Fig. 7); labial palpomere I without secondary seta; width of head capsule 1.30–1.45 (aver. 1.36, n=7) mm. Thorax: femora with 3 spiniform secondary setae. Abdomen: terga I–IV with TE_α long, nearly as long as TE_{10} (Fig. 9); urogomphi 1.05–1.20 times as long as width of tergum IX, with 9 long setae, UR_α absent (Fig. 10).
SECOND INSTAR. Head: antennomere I without secondary seta, antennomere II with one secondary seta; width of head capsule 0.84–1.10 (aver. 0.94, n=7) mm. Thorax: femora with 2 spiniform secondary setae. Abdomen: TE_α about two thirds of TE_{10} length.
FIRST INSTAR. Head: index width/length = 1.40–1.45; egg bursters forming a ridge composed of very small, blunt teeth, more spaced proximad, reaching FR_2, PA_4 at most one third of the egg burster's length (Fig. 1); coronal suture about one third of the antennomere IV length; width of head capsule 0.63–0.67 (aver. 0.65, n=7) mm. Abdomen: tergal setae of the posterior row about four times as long as setae of the anterior row (Fig. 8); urogomphi 1.2–1.3 times as long as width of tergum IX.

Amara (*Amara*) *littorea* C. G. Thomson, 1857
(Figs 11–20)

COLOUR. Head, thoracic and abdominal terga rusty brown, in first and second instars head and pronotum darkened.
THIRD INSTAR. Head: cephalic capsule transverse (index width/length = 1.45–1.60), subquadrate, slightly narrowed in apical fifth; cervical grooves distinct, reaching space between PA_3 and PA_5 dorsally, short ventrally, not reaching PA_{15}, coronal suture half as long as antennomere IV; nasale with 6 large teeth, the two lateral teeth separated from the four medial teeth by an incision of about one tooth width (Fig. 14); mandibles nearly twice as long as basal width, with one longer and three shorter secondary setae (Fig. 16) antennomere I with one short secondary seta, antennomere II with two secondary setae, labial palpomere I without secondary seta; width of head capsule 1.12–1.20 (aver. 1.15, n=5) mm. Thorax: femora with 3 spiniform secondary setae. Abdomen: terga I–IV with TE_α long, nearly as long as TE_{10} (Fig. 19); urogomphi nearly as long as width of tergum IX, with 10 long setae, UR_α long, about two thirds of UR_β length (Fig. 20).
SECOND INSTAR. Head: coronal suture shorter than half length of antennomere IV; antennomere I without secondary seta, antennomere II with only one secondary seta; width of head capsule in two specimens 0.80 and 0.84 mm. Thorax: femora with 2 spiniform secondary setae. Abdomen: TE_α about half as long as TE_{10}.
FIRST INSTAR. Head: index width/length = 1.35–1.45; cervical grooves nearly reaching PA_{15} ventrally; egg bursters forming a ridge composed of very small blunt teeth, being more spaced proximad (Fig. 11), not even twice as long as PA_4, but reaching over FR_2; coronal suture short, one third of the antennomere IV length; width of the head capsule 0.55–0.58 (aver. 0.56, n=4) mm. Abdomen: length of tergal setae in the anterior row about one fourth of those in posterior row (Fig. 18); urogomphi 1.2–1.4 times as long as width of tergum IX.

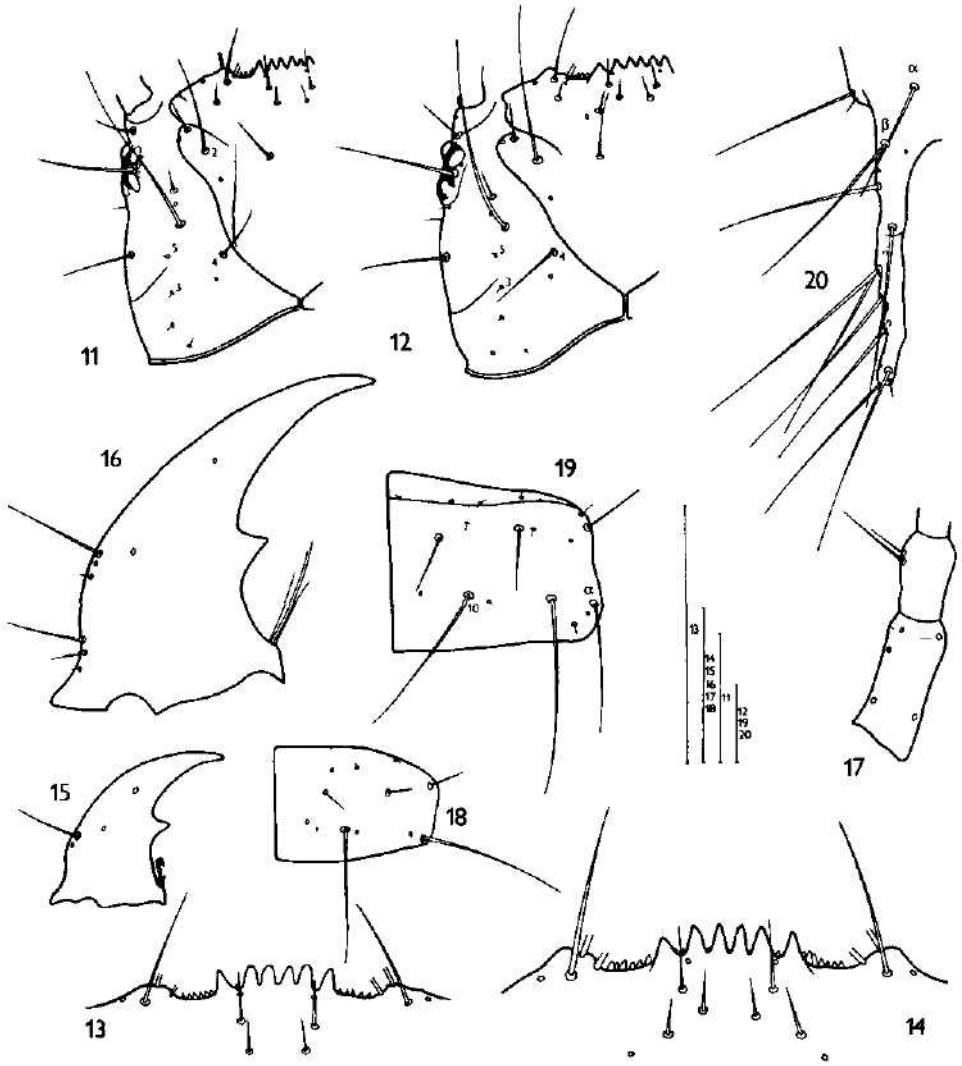


Figs 1–10. *Amara* (*A.*) *familica* Zimmermann. 1: cephalic capsule of L_1, 2: cephalic capsule of L_3, 3: mandible of L_1, 4: mandible of L_3, 5: nasale of L_1, 6: nasale of L_3, 7: antennomeres I+II of L_3, 8: abd. tergum IV of L_1, 9: abd. tergum IV of L_3, 10: tergum IX and urogomphus of L_3. Scales = 0.2 mm.

Amara (*Amara*) *proxima* Putzeys, 1866
(Figs 21–30)

COLOUR Head brown to rusty brown, in first and second instar thoracic and abdominal terga brown-grey

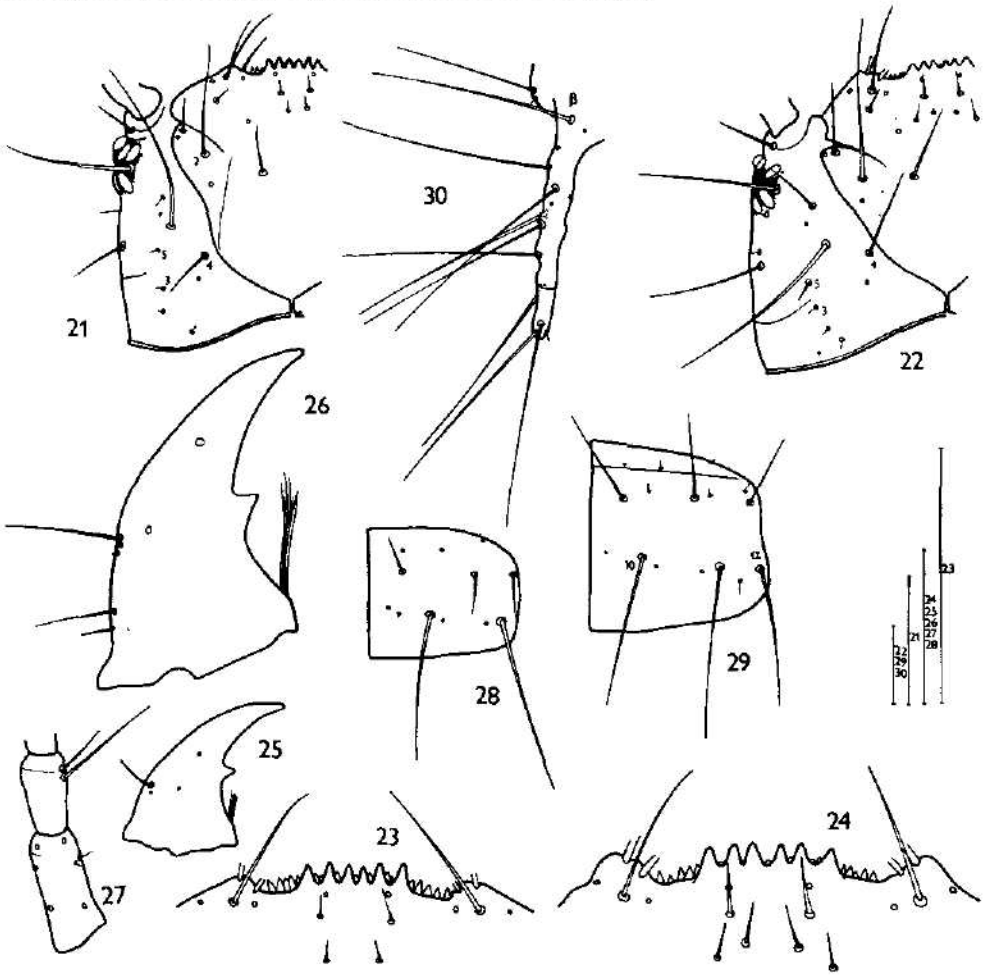
THIRD INSTAR Head cephalic capsule transverse (index width/length = 1 45–1 60), sides slightly convex, cervical grooves shallow, reaching dorsally space between PA_3 and PA_5, short ventrally,



Figs 11–20 *Amara* (*A*.) *littorea* C G Thomson 11 cephalic capsule of L_1, 12 cephalic capsule of L_3, 13 nasale of L_1, 14 nasale of L_3, 15 mandible of L_1, 16 mandible of L_3, 17 antennomeres I+II of L_3, 18 abd tergum IV of L_1, 19 abd tergum IV of L_3, 20 tergum IX and urogomphus of L_3 Scales = 0 2 mm

not reaching PA_{15}; coronal suture short, about one third of the length of antennomere IV; nasale with six large teeth, the two and two inner teeth slightly less spaced (Fig. 24); mandibles with one longer and with two or three shorter secondary setae (Fig. 26); antennomere I bearing one, rarely two short secondary setae, antennomere II with two secondary setae; labial palpomere I without secondary seta; width of head capsule 1.03–1.18 (aver. 1.12, n=5) mm. Thorax: femora with 3 spiniform secondary setae. Abdomen: terga I–IV with TE_{α} long, nearly as long as TE_{10} (Fig. 29); urogomphi slightly shorter than or about as long as the width of tergum IX, with 9 long setae, UR_{α} absent or minute (Fig. 30).

SECOND INSTAR. Head: antennomere I without secondary seta, antennomere II with one secondary seta; width of head capsule 0.76–0.84 (aver. 0.80, n=6) mm. Thorax: femora with two spiniform secondary setae. Abdomen: TE_{α} about one third of TE_{10} length.



Figs 21–30. *Amara* (*A.*) *proxima* Putzeys. 21: cephalic capsule of L_1, 22: cephalic capsule of L_3, 23: nasale of L_1, 24: nasale of L_3, 25: mandible of L_1, 26: mandible of L_3, 27: antennomeres I+II of L_3, 28: abd. tergum IV of L_2, 29: abd. tergum IV of L_3, 30: tergum IX and urogomphus of L_3. Scales = 0.2 mm.

FIRST INSTAR. Head: index width/length = 1.30–1.35; cervical grooves nearly reaching PA_{15} ventrally; egg bursters forming a ridge composed of very small blunt teeth, more spaced proximad, not even twice as long as PA_4, but reaching over FR_2 (Fig. 21); coronal suture only about one fourth of the antennomere IV length; width of head capsule 0.53–0.57 (aver. 0.55, n=7). Abdomen: tergal setae of the posterior row about four times as long as setae of the anterior row (Fig. 28); urogomphi 1.1–1.2 times as long as width of tergum IX.

Differential diagnosis of the subgenus *Amara* Bonelli, 1810

The recent knowledge (Arndt 1991, Luff 1993) and our new data enable to determine the differential diagnosis of the subgenus *Amara* in the larval stage as follows.

Nasale with 6 large teeth in the upper row; egg bursters forming two subparallel keels composed of very small blunt teeth; retinaculum at about middle of mandible; cervical grooves on dorsal and ventral surface of head capsule, ventrally extending almost to the seta PA_{15}; coronal suture distinct, about as long as or longer than diameter of antennomere IV; labial palpomere I without secondary setae. Abdominal sternite IX without median setae except those of the posterior row; urogomphi with 6 to 10 long setae.

DEVELOPMENT AND BREEDING TYPE

Amara (A.) famelica

REARING. Four pairs were kept in two containers from May 8 to November 15, 1990 (food: oat flakes+pieces of *T. molitor* larvae, natural light conditions, m. t. 20.7 °C, min. 12 °C, max. 25 °C); no eggs have been laid. After hibernation 2M, 2F and 1M, 1F were kept from March 15 to June 17 under similar conditions as in 1990. Eighty-three eggs or larvae have been found in containers from April 2 to May 20 (mean fertility pro female = 28 eggs). Three types of diet were offered to the larvae: oat flakes, oat flakes+*T. molitor* larvae, *T. molitor* larvae. Table 1 shows the influence of various diets upon the developmental time of the larval stage, table 2 shows the influence of food type upon the mortality in the larval and pupal stages. All three types of diet enable emergence of adults. There are no significant differences in the developmental time spent in larval and pupal stages, influenced by the offered food type. Nevertheless, both stages lasted the shortest time by the mixed diet of larvae. In average all three larval instars developed 37 days by m. t. 18.2 °C (min. 28, max. 51), the third instar more than twice as long as the first and/or second instar; the pupal stage lasted in average 11 days (min. 9, max. 12) by m. t. 19.1 °C. On the other hand, the significantly lowest mortality show the larvae on mixed vegetable+insect diet (Tab. 2). The third instar larvae present the highest mortality on all food types.

Amara famelica belongs to the species without larval dormancy, with the early spring propagation.

Amara (A.) littorea

REARING. Was not very successful. In 1993 (2M, 4F kept from April 29), in 1994 (2M, 4F kept from March 14) and in 1996 (1M, 1F kept from April 24) no eggs were laid (found) in the laboratory. In 1995 only $2L_1$ were found on May 5 from 1M, 3F, kept from April 25 to July 13. In 1997 4M, 2F were found in Praha-Radotín and kept from April 3 to June 16 in the laboratory at m. t. 20 °C (min. 13 °C, max. 25 °C) and under natural light conditions; food of adults: pieces of *T. molitor* larvae+oatflakes, food of larvae: pieces of *T. molitor* larvae. Six L_1 and five L_2 were found from April 28 to May

Tab. 1. *Amara famelica* Zimmermann developmental time (in days) in relation to the larval diet

Amara famelica	Diet	n	mean temp	mean time	SD	min	max.
First instar	OF	6	17.7	8 166	± 1 329	6	10
	OF+TM	15	18.6	6 533	± 0 639	6	8
	TM	11	17.6	7 000	± 1.183	6	9
Second instar	OF	13	17.7	9 000	± 1.527	7	12
	OF+TM	16	18.1	8.000	± 1.897	4	11
	TM	18	17 4	8.500	± 0.985	7	10
Third instar	OF	6	18.2	19 833	± 2 401	16	23
	OF+TM	9	17 9	21.333	± 3 354	15	25
	TM	7	18.9	20.428	± 7.849	15	36
Pupal stage	OF	5	19 0	11.200	± 1.095	10	12
	OF+TM	8	18.9	11.000	± 0 755	10	12
	TM	6	19 4	11.166	± 1 169	9	12
All larval instars	OF	3	18.1	40.333	± 1 154	39	41
	OF+TM	9	18.0	36.222	± 4 381	30	43
	TM	6	18 6	36.500	± 8 826	28	51

OF = oat flakes, TM = *Tenebrio molitor* larvae

5. The development of $1L_1$ lasted 7 days at m.t. 21.4 °C (min. 18 °C, max. 23 °C). Three L_2 developed 6, 9 and 9 days at m.t. 21.4 °C (min. 17 °C, max. 24 °C). All L_3 were fixed for the taxonomic description.

Amara littorea belongs to the species without larval dormancy and with early spring propagation in its annual cycle.

Amara (A.) proxima

Rearing. Four pairs were kept in four containers from April 18 to June 19, 1995 in laboratory (food: oat flakes+pieces of *T. molitor* larvae; natural photoperiod; m.t. 21 °C, min. 17 °C, max. 25 °C). Sixty-two eggs and/or first instar larvae were found from April 28 to May 15, fertility of separate females: 2, 15, 29, 16 eggs; (some) females laid probably eggs in the field, before their transfer in the laboratory. Larvae were feed only on insect diet (*T. molitor* larvae) and their mortality was considerable (Tab. 4): from the 20 first instar larvae only 2 males finished their development (mortality 90%). Both larval and pupal stage have a short developmental time (Tab. 3). Third larval instar developes, as a rule, more than twice as long as the first and/or the second instar. Development of two males lasted (without the egg stage) 39 and 48 days (m. t. 21.5 °C).

Amara proxima developes without larval dormancy, with the early spring propagation.

Tab 2 *Amara famelica* Zimmermann mortality in relation to the larval diet

Diet	First instar n	Second instar n of dead spec.	Third instar n of dead spec	Pupal stage n of dead spec.	Adult stage n	Mortality rate
OF	11	1	4	1	5	54.5 %
OF+TM	12	0	3	1	8	33 3 %
TM	13	1	5	1	6	53 8 %

OF = oat flakes, TM = *Tenebrio molitor* larvae

Tab 3 *Amara proxima* Putzeys developmental time (in days)

A proxima	n	mean temperature	mean time	SD	min	max.
First instar	14	21.1	6 786	± 0.893	6	9
Second instar	22	21.0	8.136	± 1 207	7	10
Third instar	6	22.1	17.833	± 2 639	14	21
Pupal stage	2	21.3	10.0	± 0 000	10	10
L_1 – Adult stage	2	21.5	43.5	± 6 363	39	48

Discussion

It is commonly assumed, *Amara* larvae are probably primarily carnivorous (Luff 1993). Burakowski (1967) gives an account of the predatory diet in larvae of *A. makolskii* (= *A. pseudocommunis* Burakowski, 1957) in both field and laboratory conditions, despite the primarily phytophagous habit of the adults of the same species. Burakowski even supposes the phenological correlation of sexual activity of *A makolskii* with the ripening and falling of birch seeds in late summer.
On the other hand, Bracht Jorgensen & Toft (1997) experimentally proved that *Amara similata* Gyllenhal, 1810 is primarily granivorous throughout the whole life cycle. Seeds as food were found to be of high value and insects of low value both for adults and larvae. The larval feeding experiment shows that the larvae are even more dependent on a seed diet than are adults. Larvae cannot survive on a pure insect diet. Few of the larvae on the mixed-insect diets (*Tenebrio* larvae, *Drosophila* larvae, aphids) survived the first two instars, and all died before the pupal stage. The aphids were even worse as food. None of the larvae of these diets survived the first instar.

In our laboratory stoks the mixed vegetable (oat flakes) and insect (*Tenebrio* larvae) diet was offered to the *Amara* adults. All three reared species laid eggs on this diet. If the rate of egg laying is taken as a measure of the value on the diet, then for *A littorea* the offered diet was of the lowest value. Larvae and pupae of both *A famelica* and *A. proxima* were able to survive on a pure insect diet, but in *A. proxima* the high mortality occurred. *A. famelica* larvae and pupae were able, besides on a pure insect diet, to develope also on a pure vegetable and a mixed vegetable+insect diet. Nevertheless, the shortest developmental time and the lowest mortality were found on the mixed diet.

It seems probable then the different species of *Amara*, even of the subgenus *Amara*, evolved the various diet strategy. It enables them to employ diverse food sources of the same habitat.

Acknowledgement

The author acknowledges the support of this study by the Grant Agency of the Czech Republic, Praha, Grant No 522/97/0271

Tab 4. Mortality of 20 *Amara proxima* Putzeys first instar larvae

Diet	First instar n	Second instar n of dead spec.	Third instar n of dead spec	Pupal stage n of dead spec	Adult stage n	Mortality rate
TM	6	2	6	4	2	90 %

TM = *Tenebrio molitor* larvae

REFERENCES

ARNDT E 1991 Familie Carabidae Pp 45–141 In KLAUSNITZER B (ed) *Die Larven der Kafer Mitteleuropas I Band Adephaga* Krefeld Goecke & Evers, 273 pp

BILY S 1972 The larva of Amara (Amara) curynota (Panzer) (Coleoptera, Carabidae) and notes on the bionomy of this species *Acta Entomol Bohemoslov* **69** 324–329

BOUSQUET Y 1985 Morphologie comparee de Pterostichini (Coleoptera, Carabidae) Description et tables de determination des espèces du nord-est de l'Amerique du nord *Naturaliste Can (Rev Ecol Syst)* **112** 191–251

BOUSQUET Y & GOULET H 1984 Notation of primary setae and pores on larvae of Carabidae (Coleoptera Adephaga) *Can J Zool* **62** 573–588

BRACHT JORGENSEN H & TOFT S 1997 Role of granivory and insectivory in the life cycle of the carabid beetle Amara similata *Ecol Entomol* **22** 7–15

BUCHAR J 1982 Publication of faunistic data from Czechoslovakia *Věst Čs Společ Zool* **46** 317–318

BURAKOWSKI B 1967 Biology, ecology and distribution of Amara pseudocommunis Burak (Coleoptera, Carabidae) *Annal Zool* **24** 485–526

DESENDER K 1988 The larvae of Amara aenea (DeGeer, 1774) and Amara familiaris (Duftschmid, 1812) (Coleoptera, Carabidae) *Bull Annls Soc R Entomol Belg* **124** 153–164

DESENDER K , POLLET M & GOOSSENS R 1986 The larva of Amara curta Dejean, 1828 and Amara tibialis (Paykull, 1798) (Col , Carabidae) with notes on the life cycle of both species *Biol Jb Dodonaea* **54** 104–115

HABU A & SADNAGA K 1963 Illustrations for identification of larvae of the Carabidae found in cultivated fields and paddy-fields (II) *Bull Natl Inst Agr Sci Ser C* **16** 151–179

HURKA K 1996 *Carabidae of the Czech and Slovak Republics* Zlin Kabourek, 565pp

LUFF M L 1993 The Carabidae (Coleoptera) larvae of Fennoscandia and Denmark *Fauna Entomol Scandinavica* **27** 1–176

THOMPSON R G 1979 A Systematic Study of Larvae in the Tribes Pterostichini, Morionini, and Amarini (Coleoptera Carabidae) *Arkansas Exp Sta , Bull* **837** 1–105

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Three new genera and species of Scorpiones (Buthidae) from Somalia

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Abstract *Orthochiroides* gen. n. (type species *O. vachoni* sp. n.) is related to *Baloorthochirus* Kovařík, 1996, and *Pakistanorthochirus* Lourenço, 1997, from Pakistan; *Birulatus* Vachon, 1974, from Jordan; *Butheolus* Simon, 1882, from Arabia; *Orthochirus* Karsch, 1892, from north Afrika and Arabia to India; and *Paraorthochirus* Lourenço & Vachon, 1995, from Iran. It differs from the above genera in having six pronounced keels on the tibia of pedipalps and lacking trichobothrium d2 of pedipalp femur on dorsal surface, but usually retaining it as an internal trichobotrium. *Somalicharmus* gen. n. (type species *S. whitmanae* sp. n.) is related to *Butheoloides* Hirst, 1925, from Africa; *Charmus* Karsch, 1879, from India and Sri Lanka, *Microcharmus* Lourenço, 1995, from Madagascar, and *Thaicharmus* Kovařík, 1995, from Thailand. It differs from the above genera in having the fingers shorter than the manus. *Somalibuthus* gen. n. (type species *S. demisi* sp. n.) is related to *Hemibuthus* Pocock, 1900, from India; *Isometroides* Keyserling, 1885, from Australia; and *Psammobuthus* Birula, 1911, from Tadzhikistan and Uzbekistan. It differs from the above genera in having keels on the carapace and three keels on the first throught sixth mesosomal segments.

Taxonomy, key, faunistics, descriptions, new genera, new species, Scorpiones, Buthidae, *Orthochiroides vachoni* gen. et sp. n., *Somalicharmus whitmanae* gen. et sp. n., *Somalibuthus demisi* gen. et sp. n., Afrotropic region

Designation of the basic trichobothrial pattern (alfa and beta configurations) is according to Sissom (1990).

Orthochiroides gen. n.
(Figs 1–5, 16–20, Tables 1–2)

TYPE SPECIES *Orthochiroides vachoni* sp. n.

ETYMOLOGY. Denotes affinity to the genus *Orthochirus*; masculinum in gender. This name was formed, but never published, by Max Vachon (see below).

DIAGNOSIS. The basic trichobothrial pattern is beta (Fig. 16 and Sissom 1990: 70, fig. 3.3); the third and fourth legs have well developed tibial spurs; pectines bear fulcra (Sissom 1990: 92, fig. 3.17D); the dentate margin of pedipalp-chela movable finger has granules distinct, divided into rows, and spanning the length of the finger (Fig. 20); in lateral view, the carapace is inclined downward from the median eyes to the anterior margin (Sissom 1990: 92, fig. 3.17F).

This complex of characters is exhibited only by the genera *Baloorthochirus* Kovařík, 1996 and *Pakistanorthochirus* Lourenço, 1997 from Pakistan, *Birulatus* Vachon, 1974 from Jordan, *Butheolus* Simon, 1882 from Arabia, *Orthochirus* Karsch, 1892 from north Africa and Arabia to India, and *Paraorthochirus* Lourenço & Vachon, 1995 from Iran. See Kovařík 1996: 177; Lourenço 1997: 154; Vachon 1974: 949; Simon 1882: 248; Karsch 1892: 306; Lourenço & Vachon 1995: 299.

Orthochiroides gen. n. is also characterized by the number and distribution of trichobothria on the pedipalps (Figs 16–19), seven to nine cutting edges on the movable fingers of pedipalps (Fig.

Table 1 Measurements in millimeters of *Somalicharmus whitmanae* gen et sp. n., *Orthochiroides vachoni* gen et sp n., and *Somalibuthus demisi* gen. et sp. n.

		Orthochiroides vachoni sp n male holotype	*Orthochiroides vachoni* sp. n female allotype	*Somalicharmus whitmanae* sp n. male holotype	*Somalibuthus demisi* sp. n. female holotype
Total	length	28.1	34 0	22.3	29 5
Carapace	length	3.1	3 8	2.8	3.0
	width	3.2	5.1	3.2	3.5
Metasoma	length	17.0	19.6	12 7	19.4
segment I	length	1.9	2 4	1.7	2.4
	width	2.8	3 4	2.0	2.2
segment II	length	2.3	2 6	1.9	2.7
	width	2.9	3.4	2.0	1.9
segment III	length	2.5	2 9	2.0	2.9
	width	3 0	3.5	2.0	1.8
segment IV	length	3.0	3.4	2.1	3.5
	width	3 1	3.6	2.0	1.8
segment V	length	3.6	4.1	2.3	3.8
	width	3.0	3.6	2.0	1.8
telson	length	3.2	4.1	2.3	3.7
Pedipalp					
femur	length	2 1	2.3	1.8	2.5
	width	0.9	1.0	0.9	0.9
patella	length	2.9	3 5	2.3	3.3
	width	1.3	1 5	1.1	1.1
tibia	length	4 0	4 5	3.8	4.4
	width	0 9	1.3	1.5	0.9
	height	1.0	1 3	1.7	0.9
finger mov.	length	2.7	3 0	1.9	2.7
Pectinal teeth		20 20	17·16	11:12	23·23

20), presence of four pairs of lateral eyes, shape of telson (Figs 1–3), mesosoma with one dorsal and four ventral keels, six pronounced keels on the tibia of pedipalps (Figs 18 and 19), dense granulation of nearly the entire body, and other features included in the description of *Orthochiroides vachoni* sp. n. below.

AFFINITIES. *Orthochiroides* gen. n. is easily recognized by the presence of six pronounced keels on the tibia of pedipalps. From the genera *Orthochirus*, *Paraorthochirus*, *Baloorthochirus*, and *Pakistanorthochirus* it also differs in shape of the telson, which is highly inflated (Fig. 1). The genera *Orthochirus* and *Paraorthochirus*, which have the fifth metasomal segment punctate, are distinguished by a very different type of this ornament which, moreover, is the same in males and females (see description of *Orthochiroides vachoni* sp. n. and Figs 1–6).

The inclusion in Sissom's (1990: 97) key to genera of the family Buthidae, after adding *Baloorthochirus*, *Pakistanorthochirus*, and *Paraorthochirus* described in 1995–97, is as follows:

Carapace in lateral view with a distinct downward slope from median eyes to anterior margin (Sissom 1990 92, fig 3 17F).

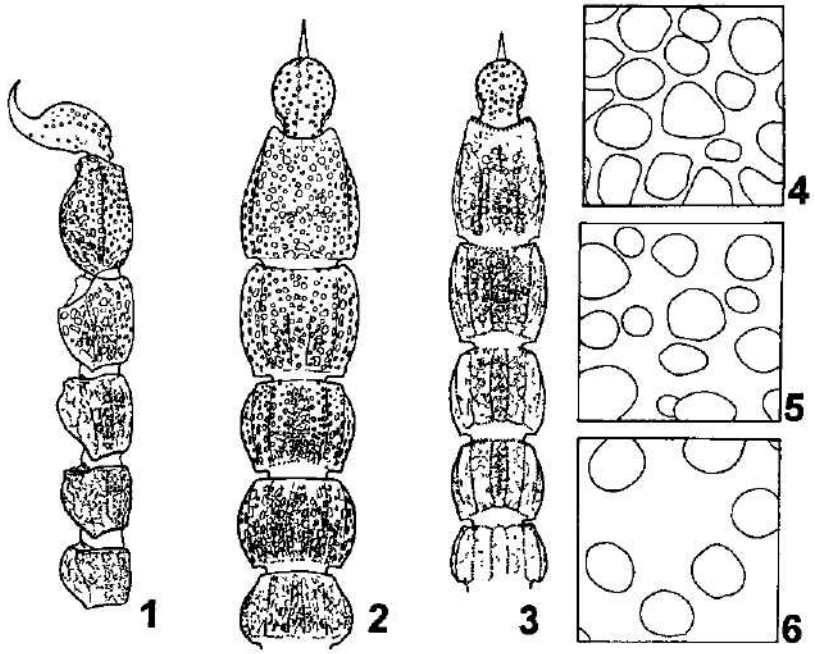
1 First and second metasomal segments without keels ..... *Birulatus* Vachon
– First and second metasomal segments with keels. 2
2 Tibia of pedipalps with pronounced keels (Figs 18 and 19). 3
– Tibia of pedipalps without keels or with feebly marked, inconspicuous keels. 4

3. Trichobothrium d2 of pedipalp femur absent on dorsal surface but usually present as internal trichobotrium (Fig 16) ..... *Orthochiroides* gen. n.
– Trichobothrium d2 of pedipalp femur present on dorsal surface. ..... *Butheolus* Simon
4. Fifth metasomal segment punctate (Fig. 6) 5
– Fifth metasomal segment granulate 6
5. Trichobothrium d2 of pedipalp femur absent on dorsal surface but usually present as internal trichobotrium (Fig. 16) ..... *Orthochirus* Karsch
– Trichobothrium d2 of pedipalp femur present on dorsal surface (Lourenço & Vachon 1995. 302 fig 10 and 303 fig. 16) ..... *Paraorthochirus* Lourenço & Vachon
6. Vesicle of telson narrow and smooth Trichobothrium d2 of pedipalp femur absent on dorsal surface but present as internal trichobotrium (Fig. 16) 7
– Vesicle of telson inflate, granulate, often with rudimental subacular tubercle (Vachon 1980: 254 planche B). Trichobothrium d2 of pedipalp femur present on dorsal surface. ..... *Butheolus* Simon
7. Movable fingers of pedipalps with nine rows of granules ..... *Baloorthochirus* Kovařík
– Movable fingers of pedipalps with six rows of granules. ..... *Pakistanoorthochirus* Lourenço & Vachon

Orthochiroides vachoni sp. n.

(Figs 1–5, 16–20, Tables 1–2)

TYPE MATERIAL Somalia, Sar Uanle, about 20 km South from Chisimaio, 00°29'48"S – 42°25'30"E, (for locality details see Messana et al. 1977 and Vanni et al 1977),18 males (holotype [MZUF No 533] and paratypes Nos 1–17 [MZUF No 536]), 11 females (allotype [MZUF No 537] and paratypes Nos 18–27 [MZUF No 538]), 9 juveniles (paratypes Nos 28–36) [MZUF No 539] All type specimens preserved in alcohol Holotype, allotype, and paratypes Nos 1–9, 20–29, 31–35 are deposited in the Museo Zoologico de "La Specola", Firenze, Italy,



Figs 1–6 (1–5.) *Orthochiroides vachoni* gen et sp n. (1–3.) Metasoma Fig 1 Male holotype. Fig 2 Female allotype Fig 3 Juvenile paratype No 28. (4–6.) fifth metasomal segment, ventral view (details 1 mm²). Fig. 4. Male holotype Fig 5. Female allotype. Fig. 6. *Orthochirus scrobiculosus* (Grube, 1873), female from Turkmenistan, Repetek.

paratype No 10 in the British Museum (Natural History), London, England, paratype No 12 in the Muséum National d'Histoire Naturelle, Paris, France, paratype No. 17 in the Department of Invertebrate Zoology, National Museum (Natural History), Prague, Czech Republic, paratype No 16 in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany, paratype No 15 in the Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany, paratype No 13 in the Zoologisches Institut und Zoologisches Museum, Universität Hamburg, and paratypes Nos 11, 14, 18, 19, 30, and 36 in the author's collection

TYPE LOCALITY. Somalia, Sar Uanle, about 20 km south of Chisimaio, 00°29'48"S – 42°25'30"E.

ETYMOLOGY. Named after the French arachnologist Max Vachon, who in 1976 examined all 38 specimens (No. VA 1405), separated them into males, females, and juveniles, and enclosed the label "*Orthochiroides* gen. nov."

DIAGNOSIS. The total length is 28.1 mm in the male holotype and 34.0 mm in the female allotype. The metasoma is shown in Figs 1–5. Measurements of the carapace, telson, segments of the metasoma and of the pedipalps, and numbers of pectinal teeth are given in Table 1. Pectinal teeth number 17–20 in males and 14–18 in females (Tab. 2).

The color is uniformly brown to black. The manus of pedipalps is brown and fingers, tibia, and tarsomeres of legs are yellow to yellowish brown. The entire metasoma is black, only the telson may be dark brown.

The pedipalps except tibia, carapace, mesosoma, coxae, and legs of adult specimens are densely covered by large granules of approximately equal size. The posterior margins of mesosomal segments dorsally terminate in granules which overlap the margins, especially in males.

The mesosoma has one poorly defined median keel on the dorsal side and four keels on the ventral side. The four ventral keels are most pronounced on the sixth and seventh segments.

The femur of pedipalps (Fig. 16) has five keels, the patella has seven keels (Fig. 17), and the tibia has six keels (Figs 18 and 19). All keels are pronounced in both sexes as well as in juveniles. For the position and distribution of trichobothria on the pedipalps see Figs 16–19. Trichobothrium d1 on the tibia of pedipalps (Fig. 17) is poorly discernible and often absent. Trichobothrium Eb3 on the manus is shifted to ventral side (Figs 18 and 19). The movable fingers of pedipalps bear seven (Fig. 20) to nine rows of granules, most frequently eight; similarly to *Orthochirus*, variability is rather high in this regard. The proximal row of granules may have zero to two external and internal granules.

The first and second metasomal segments bear 10 keels. On the third metasomal segment of males the keels are poorly indicated, and on the fourth and fifth segments there are only dorsal keels or their edges, which are rounded in females. In contrast to adults, the first four metasomal segments of juveniles bear 10 pronounced keels, and the fifth segment bears a ventral median keel and pronounced ventrolateral keels that terminate in several large granules, like in *Baloorthochirus*.

The first and second metasomal segments of males are granulated, and the third and fourth segments bear a granular network. The fifth metasomal segment is punctate (except for the dorsal

Table 2 Number of pectinal teeth in *Orthochiroides vachoni* gen. et sp. Each pecten is regarded as a unit Where both pectens are complete, they are counted twice In contrast, pectens which are obviously abnormal or incomplete are not included

	number of teeth in pecten							number of specimens
	14	**15**	**16**	**17**	**18**	**19**	**20**	
males	–	–	–	3	15	13	5	18
females	1	4	8	7	2	–	–	11
juveniles	–	–	2	6	8	2	–	9

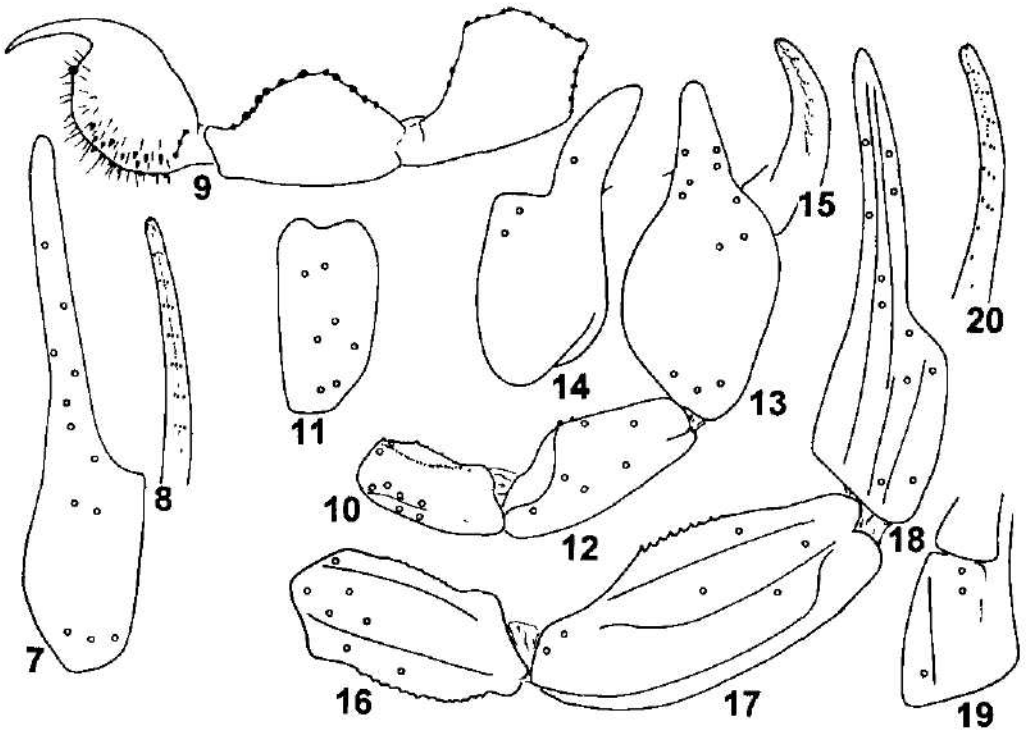
surface), but the punctae are larger than in *Orthochirus* and take much more of the surface area than the spaces separating them (Figs 1 and 4). Females have the first metasomal segment granulated, the second segment bears a granular network, and the third to fifth segments are punctate (Fig. 2). The punctae on the fifth segment are more rounded in females (Fig. 5) than in males (Fig. 4) and the surfaces separating them are smooth. In juveniles the first to fourth metasomal segments are granulated, the fifth segment bears a granular network, and only the telson of both sexes is punctate (Figs 1–3), with spaces separating the punctae always taking more surface area of the telson (Figs 1–3).

AFFINITIES. See generic affinities.

DISCUSSION. The large type series permits to discern a surprising variability and sexual dimorphism.

Similarly to *Orthochirus* (Kovařík 1996: 181), variability is pronounced in the number of rows of granules on movable fingers (7–9) and the presence and number of external and internal granules at the proximal row (0–2).

Most surprising, however, is the variation in the number of keels and punctate or granulate sculpture on the metasomal segments of both sexes and juveniles (Figs 1–3). Males have the third



Figs 7–20. (7–8) *Somalibuthus demisi* gen. et sp. n. (holotype). Fig. 7. Tibia, dorsal and external views. Fig. 8. Movable finger. (9–15) *Somalicharmus whitmanae* gen. et sp. n., holotype. Fig. 9. Fourth and fifth metasomal segments and telson. Fig. 10. Femur, dorsal view. Fig. 11. Patella, external view. Fig. 12. Patella, dorsal view. Fig. 13. Tibia, dorsal and external views. Fig. 14. Tibia, ventral view. Fig. 15. Movable finger. (16–20) *Orthochiroides vachoni* gen. et sp. n. holotype. Fig. 16. Femur, dorsal view. Fig. 17. Patella, dorsal view. Fig. 18. Tibia, dorsal and external views. Fig. 19. Tibia, ventral view. Fig. 20. Movable finger.

to fifth metasomal segments without keels, in females the keels on the third and fourth metasomal segments are poorly indicated, and juveniles before the last ecdysis (before adulthood) have 10 pronounced keels on the third and fourth metasomal segments and conspicuous ventrolateral keels on the fifth metasomal segment. Furthermore, punctate sculpture is absent in juveniles, although this character is commonly used to differentiate genera (see the key above). For instance in both sexes as well as juveniles of *Orthochirus* the fifth metasomal segment always is clearly punctate.

This surprising variability must be taken into account when dealing with the group of genera included in the key and when describing new species and genera.

The genus *Afghanorthochirus* Lourenço & Vachon (1997: 330) is not included in the above key, because I fail to see how it is supposed to differ from the genus *Orthochirus*.

Somalicharmus gen. n.

(Figs 9–15, Table 1)

TYPE SPECIES *Somalicharmus whitmanae* sp. n.

ETYMOLOGY. Denotes affinity to the genus *Charmus* and the geographic distribution; masculinum in gender.

DIAGNOSIS. The basic trichobothrial pattern is alfa (Fig. 10 and Sissom 1990: 70, fig. 3.3), the third and fourth legs have well developed tibial spurs, the sternum is subpentagonal, and the pedipalp manus has 3 Eb trichobothria on the palm (Fig. 13). This complex of characters is exhibited only by the genera *Butheoloides* Hirst, 1925 from Africa, *Charmus* Karsch, 1879 from India and Sri Lanka, *Microcharmus* Lourenço, 1995 from Madagascar, and *Thaicharmus* Kovařík, 1995 from Thailand. See Hirst 1925: 414; Karsch, 1879: 104; Lourenço 1995: 98; Kovařík, 1995: 195.

Somalicharmus gen. n. is also characterized by the number and distribution of trichobothria on the pedipalps (Figs 10–14), short movable and fixed fingers of pedipalps (Figs 13–15 and Tab. 1), wide manus (Figs 13–14 and Tab. 1), pectines with fulcra, three pairs of lateral eyes, and nine cutting edges on the movable fingers of pedipalps (Fig. 15). Other characters are given in the description of *Somalicharmus whitmanae* sp. n. below.

AFFINITIES. Inclusion in Sissom's (1990: 94) key to genera of the family Buthidae, with the genera *Thaicharmus* and *Microcharmus* described in 1995 added, is as follows:

Pedipalp chela with 3 Eb trichobothria on palm:

1 Movable finger of pedipalps longer than manus 2
– Movable finger of pedipalps shorter than manus (Figs 13 and 15) . . . . . *Somalicharmus* gen. n.
2. Telson with distinct subaculear tubercle. 3
– Telson lacking subaculear tubercle. 4
3. Cutting edges on movable fingers of pedipalps number nine (including apical row) . . . . . *Butheoloides* Hirst
– Cutting edges on movable fingers of pedipalps number 12 (including apical row). . . . . *Thaicharmus* Kovařík
4. Pectines with fulcra. . . . . *Charmus* Karsch
– Pectines without fulcra. . . . . *Microcharmus* Lourenço

Apart from the character given in the key, *Somalicharmus* gen. n. differs from the other included genera in number and distribution of trichobothria on the pedipalps (Figs 10–14 and figs 7–11 in Kovařík 1995: 191), pectines with fulcra, three pairs of lateral eyes, nine cutting edges on the movable fingers of pedipalps (Fig. 15), and other features included in the description of *Somalicharmus whitmanae* sp. n. below.

From *Charmus* and *Microcharmus* it also differs in the presence of a subaculear tooth, which is wider than in *Thaicharmus* and *Butheoloides*. Furthermore, the telson is partly covered by conspicuous, pointed granules (Fig. 9).

Somalicharmus whitmanae sp. n.
(Figs 9–15, Table 1)

TYPE MATERIAL. Holotype – a male preserved in alcohol, labeled "Somalia, El Meti" and deposited in the Museo Zoologico de "La Specola", Firenze, Italy [MZUF No. 534]. This specimen was revised in 1983 by Max Vachon under his number VA 956, and marked by him as "gen. n.".

TYPE LOCALITY. Somalia, El Meti.

ETYMOLOGY. Named after Sarah Whitman, curator at the Museo Zoologico de "La Specola", Firenze, Italy.

DIAGNOSIS. The length of the holotype is 22.3 mm. Measurements of the carapace, telson, segments of metasoma and segments of pedipalps, and numbers of pectinal teeth are given in Table 1. Pectinal teeth number 11 and 12. For the position and distribution of trichobothria on the pedipalps see Figs 10–14. Trichobothrium esb on the tibia is smaller than other trichobothria (Fig. 13).

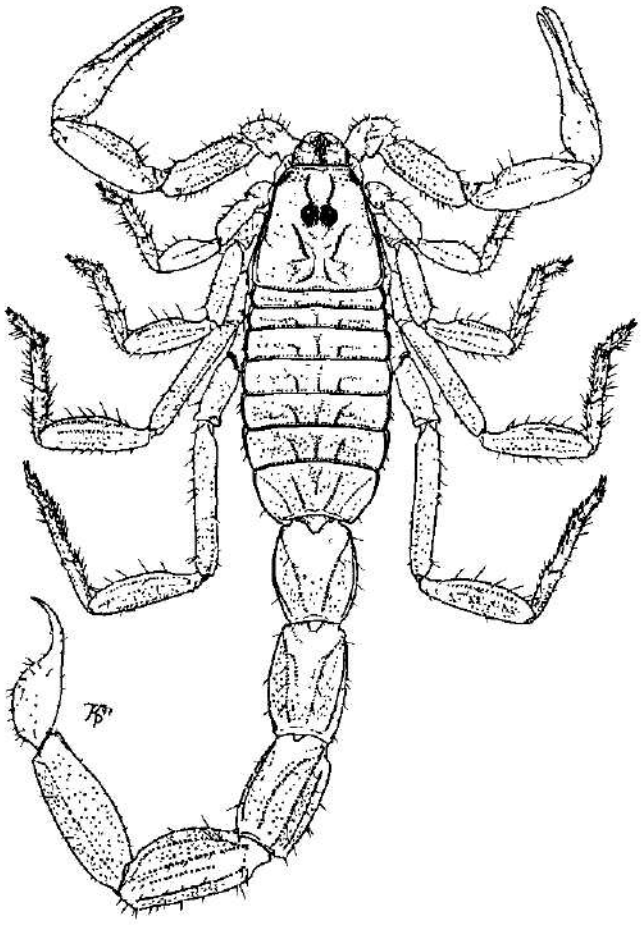


Fig. 21. *Somalibuthus demisi* gen. et sp. n. (holotype). Dorsal view.

The color is uniformly yellowish brown, only the proximity of the median and lateral eyes is black. However, due to the length of preservation in alcohol it is necessary to presume some alteration of the original color.

The entire femur and patella of pedipalps are covered with fine granules. Keels are inconspicuous, composed of but a few somewhat larger granules. The internal surfaces of femur and patella bear two to four conspicuous granules on lateral keels. The tibia of pedipalps lacks keels and is rounded and nearly smooth, with but a few isolated granules chiefly on the internal surface. The tibia is taller than wide (Figs 13–14 and Tab. 1).

The carapace lacks keels and its entire surface is evenly granulated. The median eyes are situated only 0.8 mm from the anterior margin. A deep median trough runs from them to the posterior margin.

The mesosoma is also covered with fine granules and lacks keels except for a barely discernible median keel which is indicated by more closely packed granules. The seventh mesosomal segment bears three large but low elevations which cover nearly the entire dorsal surface. The ventral surfaces of mesosomal segments are smooth, without keels and granules. The pectines bear fulcra.

The legs are less granulated, and the third and fourth legs have well developed, long tibial spurs.

All metasomal segments are granulated. The ventral sides of the first through third segments bear four keels, of which the outer ones posteriorly converge and at the hind margin of each segment connect to form the letter "u". The inner keels remain parallel and are less pronounced, being composed of isolated granules. The ventral and lateral sides of the fourth and fifth segments are granulated, rounded, and without keels. The dorsal surface of all metasomal segments bears a median trough and two lateral keels composed of several large, mutually distant granules whose size increases with each consecutive segment, i. e. they are the smallest on the first segment and the largest on the fifth, where the keels are composed of 12 to 15 granules (Fig. 9).

The telson is highly inflated, nearly spherical, with a minute subaculear tubercle. Its ventral surface is densely hirsute and covered with pronounced, pointed, dark-brown to black granules (Fig. 9).

AFFINITIES. See generic affinities.

Somalibuthus **gen. n.**

(Figs 7–8, 21, Table 1)

TYPE SPECIES. *Somalibuthus demisi* sp. n.

ETYMOLOGY. Denotes affinity to the genus *Buthus* and geographic distribution; masculinum in gender.

DIAGNOSIS. The basic trichobothrial pattern is beta (Fig. 16 and Sissom 1990: 70, fig. 3.3); the third and fourth legs have well developed tibial spurs; the pectines bear fulcra (Sissom 1990: 92, fig. 3.17D); the dentate margin of pedipalp-chela movable finger bears distinct granules divided into rows and spanning the length of the finger (Fig. 8); the entire dorsal surface of the carapace is nearly horizontal in lateral view; the cheliceral fixed finger has a single ventral denticle; and the telson lacks a subaculear tubercle (Fig. 21).

This complex of characters is exhibited only by the genera, *Hemibuthus* Pocock, 1900 from India, *Isometroides* Keyserling, 1885 from Australia, and *Psammobuthus* Birula, 1911 from Tadzhikistan and Uzbekistan. See Pocock 1900: 34; Keyserling 1885: 16; Birula 1911: 69.

Somalibuthus gen. n. is also characterized by the number and distribution of trichobothria on the tibia of pedipalps (Fig. 7); eight rows of granules on the movable fingers of pedipalps, which are not slanted and form an interrupted line (Fig. 8); three pairs of lateral eyes; the shape of telson (Fig. 21); the first throught sixth mesosomal segments with three dorsal keels (Fig. 21) and the seventh

mesosomal segment with five dorsal keels; and other features included in the description of *Somalibuthus demisi* sp n. below. The carapace bears an anterior median keel and central lateral keels (Fig. 21), and sometimes also well developed posterior lateral keels.

AFFINITIES. Inclusion in Sissom's (1990: 97) key to genera of the family Buthidae is as follows:

Telson with tubercle either very subtile or absent:

1. Carapace with keels. 2
   Carapace without keels 3
2 *First throught sixth mesosomal segments with a single keel.* . . . . . *Isometroides* Keyserling
– First throught sixth mesosomal segments with three keels . . . . . *Somalibuthus* gen. n
3. Tibiae and tarsi of first through third legs with bristlecombs along retrolateral margins. . . . . *Psammobuthus* Birula
– Tibiae and tarsi of first through third legs with setae, but not arranged as above . . . . . *Hemibuthus* Pocock

Somalibuthus demisi sp. n.
(Figs 7–8, 21, Table 1)

TYPE MATERIAL. Somalia, Sar Uanle, about 20 km South from Chisimaio, 00°29'48"S – 42°25'30"E, (for locality details see Messana et al 1977 and Vanini et al 1977), 1 female (holotype) labeled "zona 3, ora 9" (see Messana et al. 1977 151), 16 XI probably 1971, and 2 juveniles (paratypes Nos 1–2) labeled "zona 4, ora 24" and "zona 6 ora 7" (see Messana et al 1977 151), 31 V.1973. All type specimens are preserved in alcohol. Holotype [MZUF No. 535], and paratype No 2 are deposited in the Museo Zoologico de "La Specola", Firenze, Italy, and paratype No 1 is in the author's collection. These specimens were revised in 1976 by Max Vachon under his numbers VA 1397 and VA 1399, and marked by him as "genre n.".

TYPE LOCALITY. Somalia, Sar Uanle, about 20 km south of Chisimaio, 00°29'48"S – 42°25'30"E.

ETYMOLOGY. Named after my friend.

DIAGNOSIS. The length is 29.5 mm in the female holotype and 12.7 mm (without missing third through fifth metasomal segments and telson) and 15.4 mm in the juvenile paratypes Nos 1–2. Measurements of the carapace, telson, segments of metasoma and segments of pedipalps, and numbers of pectinal teeth are given in Table 1. There are 23 pectinal teeth in the holotype and 21–22 in the paratypes. For the position and distribution of trichobothria on the tibia of pedipalps see Fig. 7.

The color is uniformly yellow to yellowish brown, only the closest proximity of the median and lateral eyes is black.

The femur of pedipalps has four keels, and the patella has three keels confined to the internal surface. Other edges of the patella are rounded. The tibia of pedipalps lacks keels and is rounded and smooth.

The carapace has an anterior median keel and central lateral keels (holotype – Fig. 21), and the paratypes have also well developed posterior lateral keels.

The first through sixth mesosomal segments bear three keels, with the outer keels of each segment diverging outward. The seventh mesosomal segment bears five dorsal keels (Fig. 21). The ventral surface of all mesosomal segments is smooth, without keels and granules.

The third and fourth legs have well developed tibial spurs. The tibia and even more so the tarsomeres of legs are covered with long hairs. Especially the inner sides of tarsomeres of the third and fourth legs are densely hirsute, but the hairs are shorter than the more spaced out hairs on the outer sides of these tarsomeres.

All metasomal segments are sparsely granulated and bear conspicuous keels (Fig. 21). The first throught fourth segments have 10 keels, and the fifth segment has three keels only on the ventral surface. Other edges of the fifth segment are rounded.

The telson is slender, smooth, and lacks a subaculear tooth or tubercle (Fig 21)

AFFINITIES See generic affinities

Acknowledgements

I would like to thank Sarah Whitman of the Museo Zoologico de "La Specola", Firenze, Italy, for the loan of material, Jiří Zídek (New Mexico Tech, Socorro, USA) for translating the text, and Pavel Krásensky for drawing all the figures

REFERENCES

BIRULA A A B 1911 2 Skorpiologische Beitrage 7–8 Psammobuthus gen nov , Psammobuthus zarudnyi sp nov *Zool Anz* **37** 69–74

HIRST S 1925 On some Scorpions from Morocco, with the Description of a new Genus and Species *Ann Mag Natur Histor* **9** 414–416

KARSCH F 1879a Skorpionologische Beitrage I and II *Mit Munch Entomol Ver* **3** 6–22, 97–136

KARSCH F 1892 Arachniden von Ceylon und von Mimikoy, gesammelt von den Herren Doctoren P und F Sarasin *Berliner Entomol Ztschr* **36** 267–310

KEYSERLING E 1885 *Die Arachniden Australiens nach der Natur beschrieben und abgebildet begonnen von Dr L Koch, Part 2* Nurnberg Verlag von Bauer & Raspe, 51 pp

KOVAŘIK F 1995 Review of Scorpionida from Thailand with descriptions of Thaicharmus mahunkai gen et sp n and Lychas krali sp n (Buthidae) *Acta Soc Zool Bohem* **59** 187–207

KOVAŘIK F 1996 Baloorthochirus beevari gen et sp n from Pakistan, and taxonomic position of Orthochirus luteipes (Scorpiones Buthidae) *Acta Soc Zool Bohem* **60** 177–181

LOURENÇO W R 1995 Description de trois nouveaux genres et de quatre nouvelles especes de scorpions Buthidae de Madagascar *Bull Mus Natl Histor Natur Paris 4e ser* **17** 95–106

LOURENÇO W R 1997 A new genus and species of scorpion (Scorpiones, Buthidae) from Pakistan *Entomol Mitt Zool Mus Hamburg* **12** 153–157

LOURENÇO W R & VACHON M 1995 Un nouveau genre et deux nouvelles especes de scorpions Buthidae d Iran *Bull Mus Natl Hist Natur Paris sect A*, **17** 297–305

LOURENÇO W R & VACHON M 1997 Un nouveau genre et quatre nouvelles espèces de scorpions (Buthidae) du Moyen-Orient *Zoosystema* **19** 327–336

MESSANA G , CHELAZZI G , CHELAZZI L , ERCOLINI A , FERRARA F , MESSERI P , PARDI L & VANNINI M 1977 Researches on the coast of Somalia the shore and the dune of Sar Uanle 12 Physical environment Microclimate and Soil *Monit Zool Ital* Suppl **9** 147–181

POCOCK R I 1900 *The fauna of British India, including Ceylon and Burma Arachnida* London Taylor and Francis, 279 pp

SIMON M E 1882 Viaggio ad Assab nel Mar Rosso, dei signori G Doria ed O Beccari con il R Arviso "Esploratore" dal 16 Novembre 1879 al 26 Febbraio 1880 II Etude sur les Arachnides de l Yemen meridional *Ann Mus Civ Stor Natur Genova* **18** 207–260

SISSOM W D 1990 Systematics, Biogeography and Paleontology Pp 64–160 In POLIS G A (ed) *The biology of Scorpions* Stanford Stanford University press, 587 pp

VACHON M 1974 Etude des caracteres utilises pour classer les familles et les genres de Scorpions (Arachnides) *Bull Mus Natl Hist Natur Paris* **140** 857–958

VANNINI M , CHELAZZI G , CHELAZZI L , ERCOLINI A , FERRARA F , MESSANA G , MESSERI P & PARDI L 1977 Researches on the coast of Somalia the shore and the dune of Sar Uanle 13 Physical environment Geomorphological notes, climate and tides *Monit Zool Ital* Suppl **9** 249–271

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Embryonic sex-linked recessive lethal mutations in *Ephestia kuehniella* (Lepidoptera: Pyralidae)

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Abstract Embryonic development of the Mediterranean flour moth, *Ephestia kuehniella* Zeller, 1879 displays features typical of the lepidopteran embryogenesis with an immersed germ band We have investigated embryonic lethality caused by sex-linked recessive lethal mutations (SLRLMs; namely sl-2, sl-4, sl-6, sl-7, and sl-15), induced in this moth earlier by ethyl methanosulfonate The SLRLMs manifested themselves mostly at late phases of embryogenesis when fully formed female larvae without marked structural defects died in the egg envelopes Late embryonic lethality was also found in sl-4, but the frequency of lethal embryos in this particular mutations was lower than expected Most probably, a fraction of the sl-4 females survived until a postembryonic stage. Thus, sl-4 cannot be regarded a typical embryonic SLRLM No substantial differences in phenotype manifestation of lethality among individual SLRLMs were found Defective formation of the germ band, which led to appearance of slender larvae, occurred in a fraction of lethal eggs in the sl-6 and sl-7 In sl-2, about half of the lethal embryos died before secretion of cuticule and ingestion of the remaining yolk while the others died as fully formed larvae In sl-15, fully developed larvae were formed, they detached from the chorion and coiled up so that their dead bodies were 'u'-shaped. Recently, a balanced lethal strain are heterozygous for two SLRLMs, sl-2 and sl-15. The 'u'-shaped larvae produced by the latter mutation are an excellent marker for verifying the genetic structure of the BL-2 strain

Embryogenesis, sex-linked recessive, lethal mutations, embryonic lethality, genetic pest control, Lepidoptera, *Ephestia kuehniella*

INTRODUCTION

Many lepidopterans belong to the most harmful insect pest in agriculture and forestry. That is why particular attention has been paid to developing autocidal methods for the supressions of lepidopteran populations. Most autocidal methods currently available are based either on radiation-induced or naturally occurring sterility (for a review, see LaChance 1985). Strunnikov (1975, 1978, 1979) proposed an alternative approach, suitable against species with WZ-ZZ chromosome system of sex determination. His proposal is based on the release of males which are trans-heterozygous for two sex-linked recessive lethal mutations (SLRLMs). In the Institute of Entomology in České Budějovice, Strunnikov's method has recently been developed in a model species, the Mediterranean flour moth (*Ephestia kuehniella* Zeller, 1879), which is well known as a cosmopolitan pest of stored products but less known as the former model organism in genetics (Robinson 1971, Caspari & Gottlieb 1975, Leibenguth 1986). In the moth, a balanced lethal strain has been constructed (Marec 1990, 1991, Marec & Mirchi 1990); the strain, called BL-2, produces the trans-heterozygous males required for introducing lethal factors into wild populations (Marec et al. 1996).

For field application of Strunnikov's method, it is preferable to use such SLRLMs which manifest themselves during embryogenesis. Thus, already the number of hatched larvae, these being the

harmful stage, can be significantly reduced. During developing the BL-2 strain in *E. kuehniella*, a total of 30 different SLRLMs were induced by the ethyl methanesulfonate and isolated using the sex-linked recessive mutation dz („dunkles Zentralfeld", Kühn 1939). The marker dz was also used for mapping the isolated SLRLMs (Marec 1989, 1990, 1991). The aim of the present paper is to characterize five selected embryonic SLRLMs of *E. kuehniella*, and compare lethal embryos with normal developing ones. Two of the selected SLRLMs, sl-2 and sl-15, have been used for construction of the BL-2 strain (Marec 1991). The detailed studies of Sehl (1931) and Maschlanka (1938) on embryogenesis of *E. kuehniella* served us as basis for embryological evaluation.

MATERIAL AND METHODS

Insects

The following SLRLMs were examined: sl-2, sl-4, sl-6, sl-7, and sl-15 (for detail characteristics, see Marec 1990, 1991). Briefly, these mutations are maintained in single-pair cultures by crosses between phenotypically wild-type males and dz females. The male parents, which are the homogametic sex with sex chromosomes ZZ, are heterozygous for a SLRLM, the other chromosome Z is marked with the mutation dz. In progeny of the crosses, lethal embryos occur in about 25% of the egs laid, representing a half of the female progeny hemizygous for the SLRLM. Consequently, the sex-ratio between the male and female progeny is shifted to 2:1. The specific lethality of the embryos in the SLRLMs was compared with normal embryonic development in the laboratory wild-type strain C (WT-C: for its origin, see Marec 1990).

Rearing

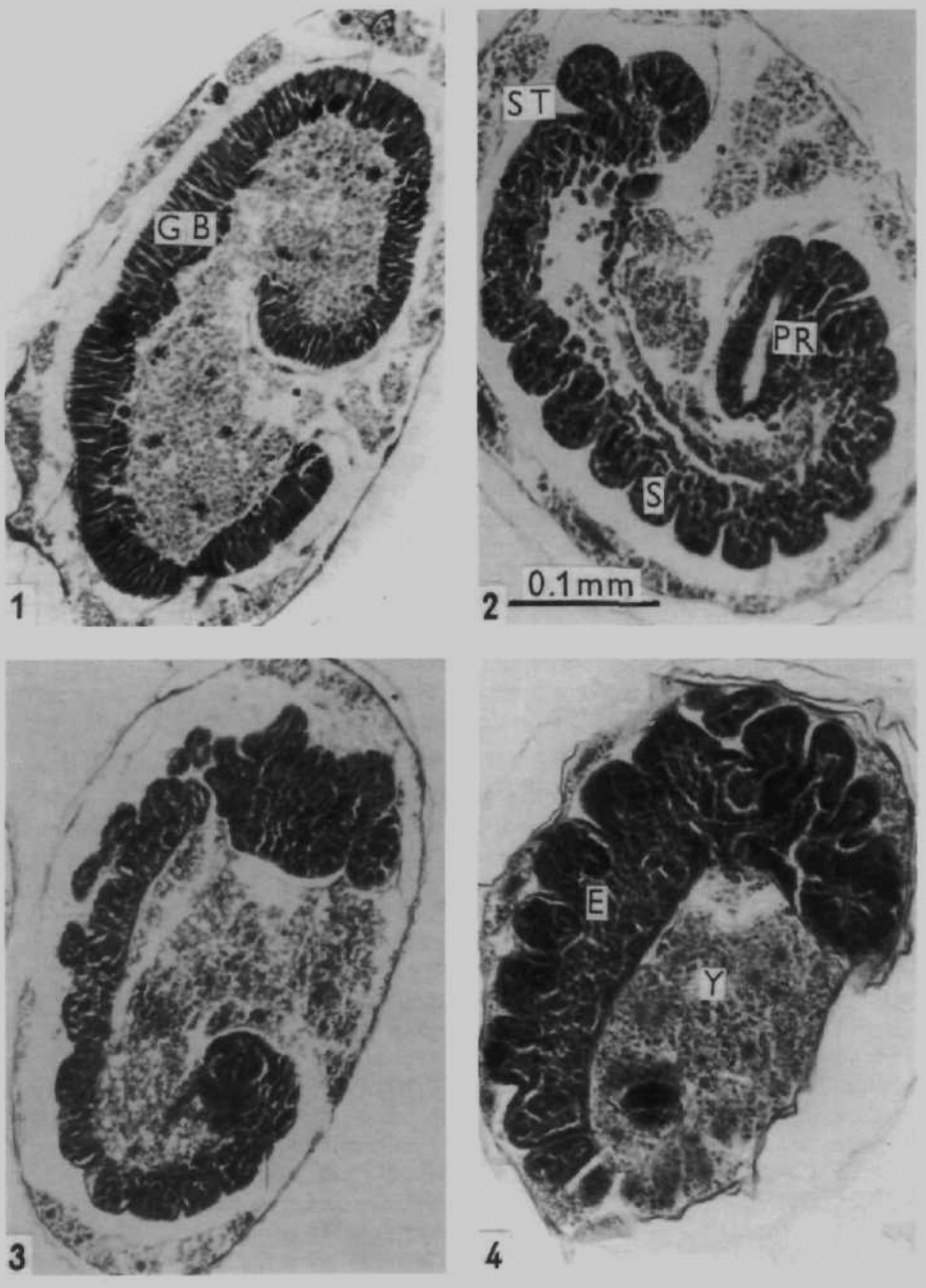
Cultures were reared on milled wheat grains supplemented with a small amount of dried yeast, at 25–27C, 60–70% r h with a 12/12 light regime. Details about the rearing method and insect handling are given by Marec (1990).

Preparations

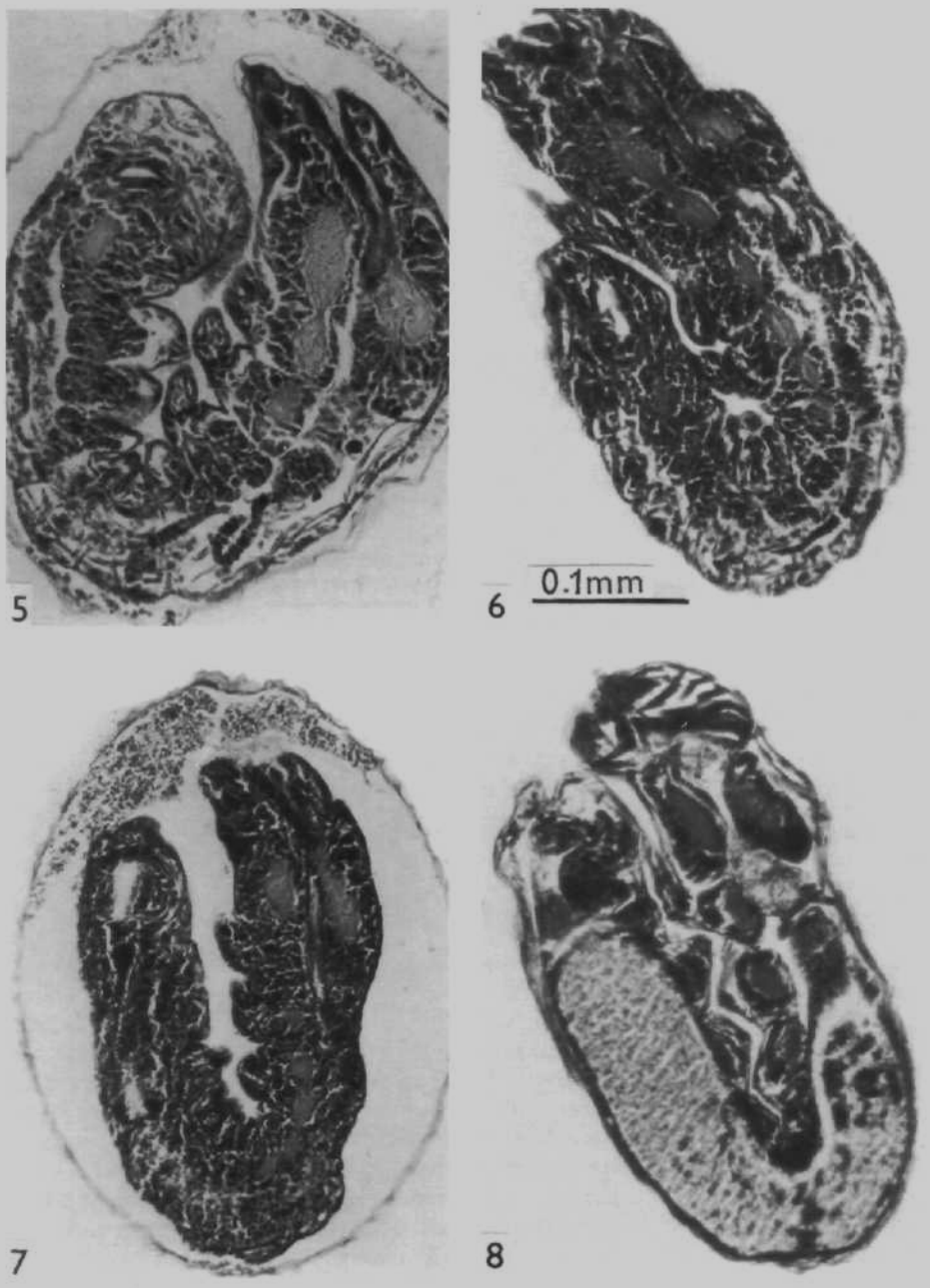
Mated females individually laid eggs in plastic Petri-dishes. For timing of the single-pair egg collections, the females were placed into new Petri-dishes each 8 hrs. At different intervals, eggs were removed from plastic surface of the dishes using metal needles and transferred into fixative. In each SLRLM line as well as in WT-C strain, a total of about 800 eggs were examined. For light microscopic (LM) preparations, eggs were fixed in the Huettner's fixative (40% formaldehyde, ethanol, acetic acid, and distilled water at the ratio of 6:16.1.30). Then their chorion was removed using fine tungsten needles and dissected embryos proceeded by usual histological procedures. Afterwards 4–6 µm thick paraplast sections were stained with Mayer's hematoxylin. For scanning electron microscopic (SEM) preparations, eggs were fixed in a 1 1 mixture of paraformaldehyde and glutaraldehyde. Dissected embryos were consecutively passed through 96% and 100% ethanol, left in amylacetate for 15 minutes, desiccated using the critical point method with CO_2, and coated with gold. Preparations were observed and photographed in a Tesla BS 300 scanning electron microscope, operated at 9 KV.

RESULTS

Cleavage divisions of a newly formed zygote take place within the yolk mass soon after syngamy of male and female pronuclei. When intralecital cleavage is over, cleavage energids migrate into the periplasm, where they form a syncytial periblast. Some cleavage nuclei remain in the yolk as vitellophages. When the division of the superficial nuclei ceases and the cellular membranes form, the syncytial periblast changes into the uniform cellular blastoderm. The embryonic primordium differentiates on the ventral side of the yolk mass as a wide transversally orientated germ band. Columnar aggregated cells of germ band soon separate from the attenuated cells of extra-embryonic blastoderm. The wide embryonic primordium, extended across the ventral side of the yolk with his edges curling dorsally, is subsequently immersed in the yolk mass and extra-embryonic blastoderm gives rise to the embryonic membranes. Then the germ band elognates forming a pair of head lobes at the anterior part and orientates longitudinally (Figs 1 and 2). Longitudinal growth of the germ band is connected with gastrulation and segmentation. The stomodaeum invaginates between the head lobes when elognation begins, while invagianion of the proctodaeum proceeds later. The head and thorax are orientated ventrally and the abdomen curves over the posterior pole and along the dorsal surface of the egg (Figs 2 and 3). Elongation is followed by subsequent shortening and



Figs 1–4. LM micrographs of *E. kuehniella* embryos (wild type), fixed in Huettner fixative and stained with Mayer's hematoxylin. Fig. 1 – formation of the germ band (GB) in the 8 hrs old embryo. Figs 2–3 – elongation and segmentation of the embryo in the age of 20 or 24 hrs, respectively. ST, stomodaeum; PR, procodaeum; S, segments. Fig. 4 – shortening of the embryo (E) and beginning of organogenesis in the age of 48 hrs. Y, yolk.



Figs 5–8. LM micrographs of *E. kuehniella* embryos, fixed in Huettner fixative and stained with Mayer's hematoxylin. Figs 5–6 –Revolution of the embryo and completion of its development in the age of 72 or 78 hrs, respectively (wild type). Fig. 7 – a slender larva of the lethal mutation *sl-7*. Fig. 8 – a 'u'-shaped larva of the lethal mutation *sl-15*.

Table 1. Characterization of individual sex-linked recessive lethal mutations (SLRLMs) according to their embryonic death. [a]Mean egg hatchability was calculated from previous experimental data on chracterization of the SLRLMs (see Table 4 in Marec 1990, and Table 1 in Marec 1991)

SLRM	Classification of unhatched eggs				Mean egg hatchability[a]	
	Non-developing eggs	Occurrence of slender larvae	Larvae died before ingestion of yolk	Fully formad larvae died	No. of pairs n	M±SD %
sl-2	(+)	–	++	++	16	63.7±5.3
sl-4	(+)	–	–	+++	14	71.1±6.0
sl-6	(+)	+	–	+++	19	67.3±5.7
sl-7	+	++	(+)	+++	16	64.4±5.8
sl-15	(+)	–	–	++++	12	64.8±2.6
Control	(+)	–	–	(+)	22	85.2±7.1

provisional dorsal closure of the embryo, accompanied by the beginning of organogenesis (Figs 4 and 10). At this stage, the short and tubular embryo lies with his convex ventral surface free within the amniotic cavity surrounded by a yolk-filled amnio-serosal space. Shortening of the embryo is followed by marked embryonic movements during which the embryo changes its position and orientation within the eggs (Figs 5, 6, 11, 12, 13). Then the embryo grows further and reverses its curvature, with a convex dorsal surface (Fig. 14). The definitive dorsal closure arises from the spreading lateral strands of ectoderm The embryo increases further its length as the remaining yolk is swallowed. Late embryogenesis is followed by the secretion of the cuticle, and the tracheae are filled with gas. The embryo breaks the amnion and ingests the rest of yolk. After the completion of histodifferentiation and growth of the embryo, the cuticle is being pigmented and sclerotized. A fully grown larva, which occupies the whole egg space, hatches at 4–4.5 days (Fig. 15).

Embryonic lethality

Data on embryonic lethality and egg hatchability in the SLRLM lines as well as the WT-C control crosses are summarized in Table 1. In single-pair cultures of the WT-C strain, approximately 85% eggs hatched in average. A detailed analysis of eggs in the control sample revealed two types of unhatched eggs, both occurring at a relatively low frequency: non-developing eggs and eggs with fully formed dead larvae. The former were most probably non-fertilized eggs that were also found at similar frequencies in each SLRLM line examined. The latter represented a probably non-specific embryonic lethality that occurred in very late phases of embryogenesis.

In egg collections the SLRLM lines, about 25% specific embryonic lethality was expected. Correspondingly, the mean hatchability of eggs was reduced. The SLRLMs manifested themselves mostly at late phases of embryogenesis when fully formed female larvae without marked structural defects died in the egg envelopes. The late embryonic lethality was also found in the sl-4, however, the frequency of lethal embryos in this particular mutation was rather lower than the expected one. Most probably, a fraction of the sl-4 females survived until a postembryonic stage of their development. Thus, the sl-4 cannot be regarded a typical embryonic SLRLM (cf. Marec 1990). No substantial differences in manifestation of lethality among individual SLRLMs were found. Defective formation of the germ band, which obviously led to the appearance of the slender larvae, occurred in a fraction of lethal eggs in the sl-6 and sl-7 (Fig. 7). In the sl-7, about half of the lethal embryos died before secretion of cuticle and ingestion of the remaining yolk, the other half died as fully formed larvae. In the sl-15, almost all the lethal eggs contained fully developed larvae; the larvae successively detached from the chorion and coiled up so that their dead bodies were 'u'-shaped (Figs 8 and 16).

DISCUSSION

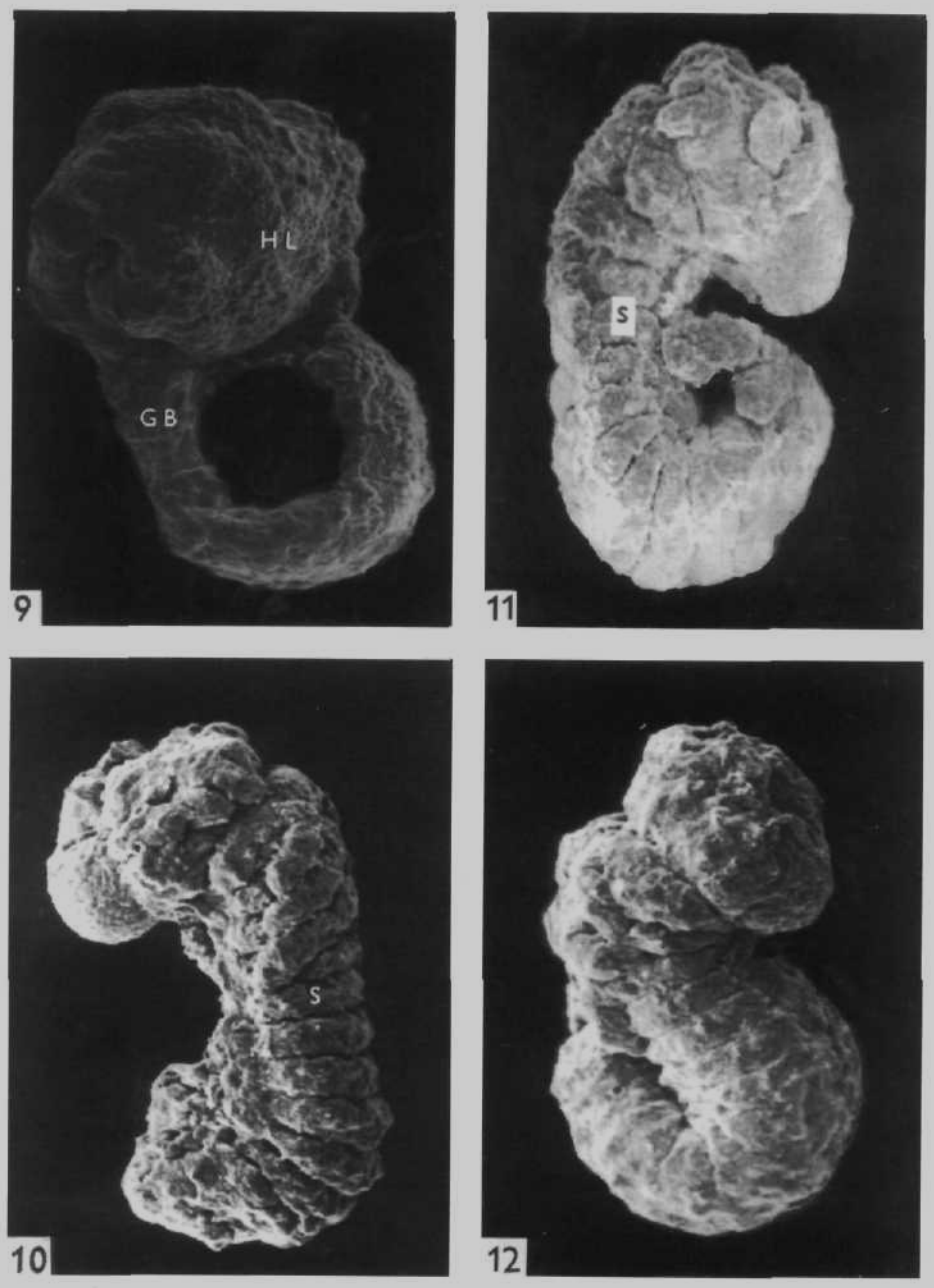
The course of embryonic development in *Ephestia kuehniella* expresses the typical features of lepidopteran embryogenesis as described by Sehl (1931), Maschlanka (1938), Red & Day (1966), Anderson & Wood (1968), Anderson (1972), Crochard (1977), etc.

It is well known that early development is not dependent on the expression of the zygotic genome (Anderson & Lengyel 1979). During early embryogenesis genetic information expressed in newly synthesized proteins is most likely maternal in origin. Early cleavage is dependent on maternal RNA until the blastoderm stage. From the blastoderm stage on, embryonic transcription substitutes increasingly the maternal transcripts which are then no longer required for further development (Jäckle & Kalthoff 1979). Garcia-Bellido & Moscoso del Pedro (1979) confirmed the importance of maternal gene activity for embryogenesis. It emerges from genetic evidence that a large number of genes are active during oogenesis and embryogenesis. LaChance et al. (1977) stated that eggs of the house fly fertilized with sperm carrying up to 70% of different deficiencies of the autosomes can develop the prehatching stage (when genes responsible for syngamy, cleavage and other essential phases of embryonic development are preserved).

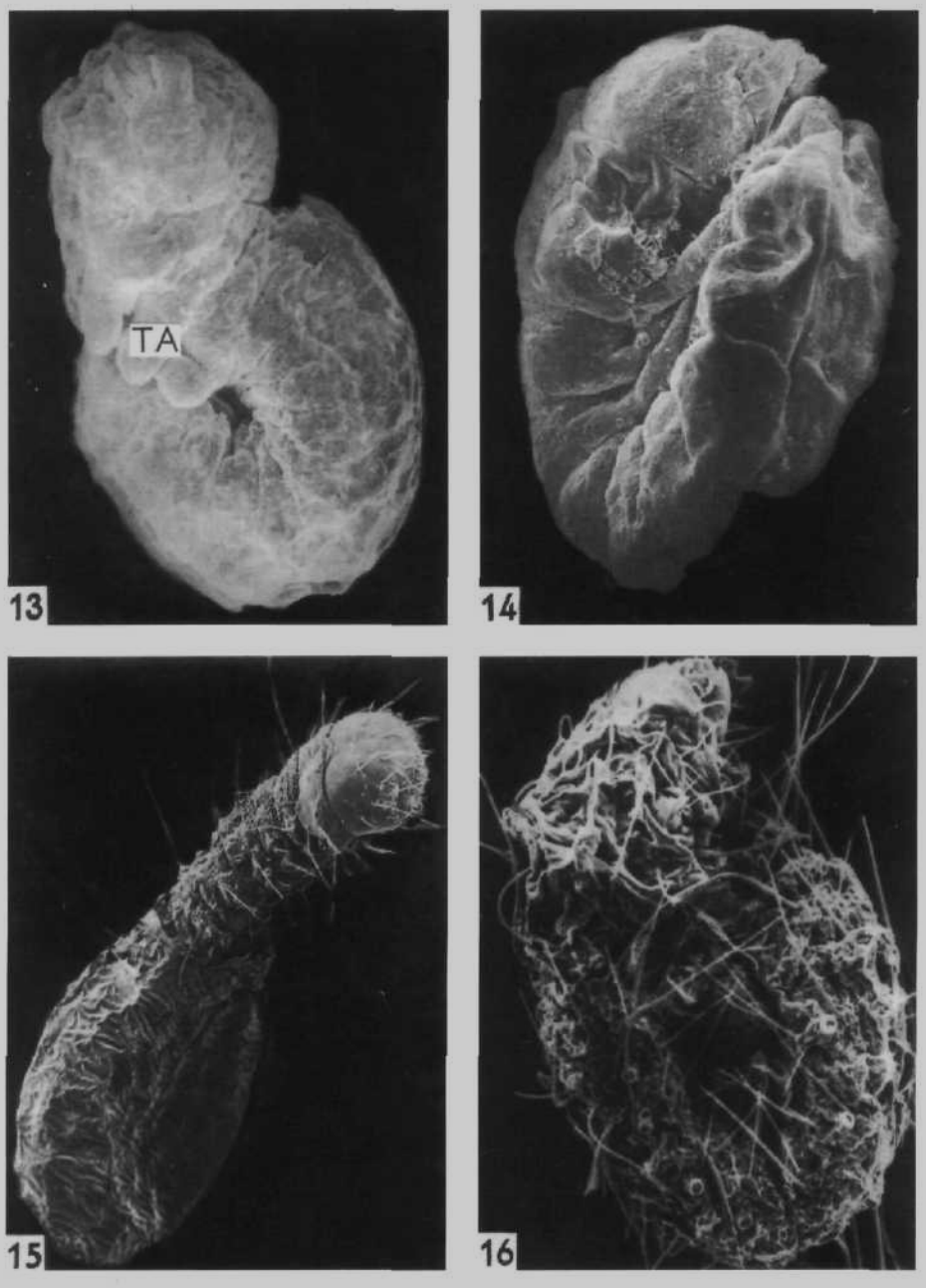
Lepidopteran eggs are believed to be incompletely determined. Such eggs are capable of considerable regulations following experimental interference in early stages but the power is lost much sooner that in indeterminate eggs (Johannsen & Butt 1941). Kühn & Plagge (1937) showed that early gene product (of maternal origin) can into larval stages compensate for zygotic gene defects. Maschlanka (1938) revealed that after cauterization of a limited area of a egg at the stage of the cleavage division or blastoderm stage, the germ band is able to complete the segmental pattern of embryo (i. e., till the blastoderm stage the cleavage nuclei are isopotent). Later cauterization led to damaged or missing segments. The results were depend on the place and time of application. Embryos in our experimental eggs mostly died at last stages of embryogenesis without any obvious morphological defects. This most probably indicates that the SLRLMs examined represent small deletions or point mutations in genes which are required at the most advanced stages of embryonic development. There is an interesting similarity to embryonic death caused by juvenoids.

Crochard (1977), who studied the ovicidal activity of juvenoids on *E. kuehniella* eggs, did not state any embryonic malformations, but embryogenesis ceased at the time of embryonic revolution or before hatching of the larvae. On the contrary, individual sex-linked recessive lethal mutations induced in the codling moth, *Cydia pomonella*, considerably varied in the stage of embryogenesis in which the derangement and inhibition of development and death of the embryo occurred (Shvedov et al. 1985, Matolín & Anisimov 1988). In Lepidoptera, the cessation of embryonic development in its advanced stages is typical for radiation-induced, dominant lethal mutations (DLMs) (LaChance 1974) that are believed to represent induced chromosomal aberrations. In this respect, Lepidoptera considerably differ from Diptera, in which early embryonic death is characteristic for induced DLMs. This is attributed to the fact that radiation-induced chromosome breaks in Diptera lead to the formation breakage-fusion-bridge cycles, whereas chromosome bridges are not seen during early embryonic development in Lepidoptera (LaChance & Graham 1984).

Recently, a balanced lethal strain of *E. kuehniella*, caled BL-2, was constructed for application in the pest control strategies (Marec 1991, Marec et al. 1996). Male moths of this strain are heterozygous for two SLRLMs, sl-2 and sl-15. When moths of this strain are intercrossed, one half of the male progeny die during embryogenesis because of being homozygous for one of the SLRLMs, either sl-2 or sl-15, depending on the genotype of female parents (see the scheme of the BL-2 strain in Marec et al. 1996). Therefore, about 25% late embryonic lethality can be observed in single-pair



Figs 9–12. SEM micrographs of *E. kuehniella* embryos (wild-type), taken at magnification of 240–390. Fig. 9 – elongated germ band (GB) with head lobes (HL) in the 16 hrs old embryo. Fig. 10 – shortening of the embryo in the age of 48 hrs. S, segments. Figs 11–12 – revolution and growth of the embryo in the age of 60 or 66 hrs, respectively. S, segments.



Figs 13–16. SEM micrographs of *E. kuehniella* embryos, taken at 200–390 fold magnification. Fig. 13 – growth of thoracic appendages (TA) in the 72 hrs old embryo (wild-type). Fig. 14 – position of the fully grown, wild-type larva in the egg, 90 hours after the egg laying. fig. 15 – the wild-type larva shortly before hatching, 92 hours after the egg laying. Fig. 16 – the dead 'u'-shaped larva of the *sl-15* mutant line.

egg collections Then the specific differences in lethality of both the sl-2 and sl-15 (see this paper) enable us to analyze the parental genotypes by routine screening of egg collections in a dissecting microscope Similarly, when males of the BL-2 strain are outcrossed with wild type females, all female progeny die during embryogenesis being hemizygous for one of the SLRLMs This result in about 50% late embryonic lethality, half of the lethal eggs represent sl-2 females, the other half sl-15 females In this respect, particularly the 'u'-shaped larvae of the latter mutation appear to be an excellent diagnostic marker for verifying genetic structure of the BL-2

In spite ot the fact that lepidopterans represent one of the largest groups of organisms and many of them belong to economically important insect pests, data concerning their embryoge-nesis as well as classical and molecular genetics are still rather inconsistent and relatively limited (Wyatt 1991) Thus, further research in this respect is needful

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REFERENCES

ANDERSON D T & WOOD E C 1968 The morphological basis of embryonic movements in the light brown apple moth, Epiphyas postvittana (Walk) (Lepidoptera Tortricidae) *Austral J Zool* **16** 763–793

ANDERSON D T 1972 The development of Holometabolous Insect Pp 165–242 In COUNCE S J & WADDINGTON C H (eds) *Developmental Systems Insects* I London and New York Academic Press, 304 pp

ANDERSON K V & LENGYEL J A 1979 Rates of synthesis of major classes of RNA in Drosophila embryos *Develop Biol* **70** 217–231

CASPARI E W & GOTTLIEB F J 1975 The Mediterranean meal moth, Ephestia kuhniella Pp 125–147 In KING R C (ed) *Handbook of Genetics Vol 3* New York Plenum Press, 874 pp

CROCHARD C 1977 *Etude experimentale du pouvior oviside de deux analogues de l hormone juvenile sur diverses pontes d insectes* Doctorat these Univ Metz (unpublished), 165 pp

GARCIA BELLIDO A & MOSCOSO DEL PRADO J 1979 Genetic analysis of maternal information in Drosphila *Nature* **278** 346–348

JACKLE H & KAITHOFF K 1979 RNA and protein synthesis in developingg embryos of Smittia spec (Chironomidae, Diptera) With *Roux s Arch Dev Biol* **187** 283–305

JOHANNSEN O A & BUTT F H 1941 *Embryology of Insect and Myriapods* New York, London Mc'Graw-Hill Book Comp , 462 pp

KUHN A 1939 Uber eine geschlechtskoppelte Mutation des Zeichnungsmunsters (dz) bei Ephestia kuhniella Z *Biol Zentralblatt* **59** 347–357

KUHN A & PLAGGE E 1937 Pradetermination der Raupenaugenpigmentierung bei Ephestia kuhniella Z durch den Genotypus der Mutter und durch arteigene und artfremde Implantate *Biol Zentralblatt* **57** 113–126

LACHANCE L E 1974 Dominant lethal mutations in insects with holokinetic chromosomes 2 Irradiation of sperm of cabbage looper *Ann Entomol Soc Amer* **67** 35–39

LACHANCE L E 1985 *Genetic methods for the control of Lepidopteran species status and potential* Washington DC ARS-28 US Department of Agriculture, 40 pp

LACHANCE L E & GRAHAM C K 1984 Insect radiosensitivity Dose curves and dose- fractionation studies of dominant lethal mutations in the mature sperm of 4 insect species *Mutation Res* **127** 49–59

LACANCE L E , RICHARD R D , JOHNSON O A & BELICH C 1977 Embryonic development in house fly eggs fertilized with genetically deficient sperm *Genetics* **86** 377–388

LEIBENGUTH F 1986 Genetics of flour moth, Ephestia kuhniella *Agric Zool Rev* **1** 39–72

MAREC F 1989 Induction of sex-linked recessive lethal mutationsin Ephestia kuehniella Zeller Pp 347–354 In TONNER M , SOLDAN T & BENNETTOVA B (eds) *Regulation of Insect Reproduction IV* Praha Academia, 539 pp

MAREC F 1990 Genetic control of pest Lepidoptera Induction of sex-linked recessive lethal mutations in Ephestia kuehniella (Pyralidae) *Acta Entomol Bohemoslov* **87** 445–458

MAREC F. 1991: Genetic control of pest Lepidoptera. Construction of a balanced lethal strain in Ephestia kuehniella. *Entomol Exp Appl* **61** 271–283.

MAREC F. & MIRCHI R. 1990. Genetic control of the pest Lepidoptera: Gamma-ray induction of translocations between sex chromosomes of Ephestia kuehniella Zeller (Lepidoptera: Pyralidae). *J. Stored Prod. Res.* **26** 109–116.

MAREC F., PAVELKA J., KOUDELOVÁ J., KŘIVAN V. & COOK P. A. 1996: *Suppression of model populations of Ephestia kuehniella* by releasing males balanced for two sex-linked recessive lethal mutations. Pp. 39–51. In: *Working Material Evaluation of Population Suppression by Irradiated Lepidoptera and Their Progeny, First FAO/IAEA Res. Co-ordination Meeting, Jakarta, Indonesia, 1995*. Vienna: International Atomic Energy Agency, 321 pp.

MASCHLANKA H. 1938. Physiologische Untersuchungen am Ei der Mehlmotte Ephestia kuehniella. *Roux's Arch Entw. Mech.* **137**: 714–722.

MATOLIN S. & ANISIMOV A. I. 1988. Embryonic sex-linked recessive lethal mutations in the codling moth, Cydia pomonella (Lepidoptera, Tortricidae). *Acta Entomol. Bohemoslov.* **85**: 116–120.

REED E. M. & DAY M. J. 1966: Embryonic movement during development of the ligth brown moth. *Austral. J. Zool.* **14**: 253–263.

ROBINSON R. 1971. *Lepidoptera Genetics*. Oxford: Pergamon Press, 367 pp.

SEHL A. 1931. Furschung und Bildung der Keimanlage bei der Mehlmotte Ephestia kuhniella Zell. *Ztschr. Morphol. Ökol. Tiere* **20**: 533–598.

SHVEDOV A. N., LITVINOVA E. M. & ANISIMOV A. I. 1985. Induction by ethylmethanesulfonate and isolation for recessive sex-linked mutation of codling moth. Pp. 23–26. In: *Genetical and Biophysical Methods in Plant Protection*. Proc. All Union Inst. Leningrad: Plant Protection, VIZR, 90 pp.

STRUNNIKOV V. A. 1975. Sex control in silkworms. *Nature* **255**: 111–113.

STRUNNIKOV V. A. 1978. [Perspectives of using balanced sex-linked lethals for the control of injurious insects]. *Genetika* **14**: 2002–2011 (in Russian).

STRUNNIKOV V. A. 1979: On the prospects of using balanced sex-linked lethals for insect pest control. *Theor. Appl. Genet.* **55**: 17–21.

WYATT G. R. 1991: Gene regulation in insect reproduction. Invertebr. *Reprod. Develop.* **20**: 1–35.

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Early Pleistocene birds of Deutsch-Altenburg, Austria

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Abstract. Early Pleistocene cave fillings Deutsch-Altenburg 4B and 2C yielded remains of 12 and 5 bird species, respectively Both the faunas are typical for mixed boreal forests of the current western Palearctic Only a single extinct species, the quail *Palaeocryptonyx donnezani* Depéret, 1892, was recorded in Deutsch-Altenburg

Aves, Biharian, Pleistocene, Austria

INTRODUCTION

Early Pleistocene record of the birds from Austria is limited to two cave fillings opened in the Hollitzer quarry between Hainburg, Bad Deutsch-Altenburg and Hundsheim in Hainburg Hills, NE Austria. The bird remains were originally described by Jánossy (1981). They are reviewed below, and supplemented by additional material.

The localities Deutsch-Altenburg 4B and Deutsch-Altenburg $2C_1$ are early Biharian in age, belonging in Rabeder's *Microtus praehintoni*-zone (DA 4B), and *Microtus pliocaenicus*-zone (DA $2C_1$), respectively (Rabeder 1972, 1973, 1981, Mais & Rabeder 1979), i. e. to the biozones $Q\,1_{1\,2}$ *sensu Horáček & Ložek (1988). The locality DA 4B is younger than DA* $2C_1$ *(Rabeder 1981).*

The sequence of Recent species follows Voous (1977). Minimum numbers of individuals were calculated according to Grayson (1984). The stratigraphy follows Horáček & Ložek (1988).

The material is deposited in the Institute of Paleontology of the University in Wien, Austria Gernot Rabeder (Wien) kindly allowed me to study the material, and contributed helpful comments on an early draft of the manuscript. I thank him very much. Most of the bones were illustrated in Jánossy (1981, pl. 1–2, and text-figures). Hence, the illustrations are not reprinted here, but references to original illustrations are given in the following species accounts.

SYSTEMATIC LIST

Falconidae

Falco tinnunculus Linnaeus, 1758

MATERIAL. DA 4B carpometacarpus sin , prox carpometacarpus dex ; MNI = 1.
FIGS. Pl 1, fig. 6, and pl 2, fig 6 in Jánossy (1981)

REMARKS. The bones from DA 4C were described and figured (photos) by Jánossy (1981). However, only an empty tube, labeled "*Falko* [sic!] *tinnunculus atavus*", was found in the collection. Nevertheless, the figures and measurements published by Jánossy (1981) allow to confirm his identification of these bones at the species level.

Phasianidae

Tetrao tetrix Linnaeus, 1758

MATERIAL DA 2C prox carpometacarpus dex., prox tibiotarsus sin., MNI = 1
MEASUREMENTS Tibiotarsus: distal width = 9.2 mm, tarsometatarsus proximal width ≅ 10.0 mm.

REMARKS. These bones were not available to Jánossy (1981).

Palaeocryptonyx donnezani Depéret, 1892

Palaeocryptonyx donnezani Depéret, 1892: 691 (figured by Depéret 1897)
Francolinus Čapeki Lambrecht, 1933: 433
Francolinus capeki Brodkorb, 1964: 320 (spelling emended).
Plioperdix capeki Mlíkovský, 1995: 116 (new combination)

MATERIAL DA 4B: 3 premaxillae, 2 humeri dex., prox. humerus dex., dist. humerus dex., prox. ulna sin., carpometacarpus sin., prox. carpometacarpus sin., 2 carpometacarpi dex., phalanx 1 digiti 2 alae dex., 4 dist. tarsometatarsi sin., MNI = 4. DA 2C: prox. humerus dex., dist. humerus dex., carpometacarpus sin., prox. carpometacarpus sin., 3 dist. tarsometatarsi sin., 2 dist. tarsometatarsi dex., MNI = 3
FIGS. Pl. 1, figs. 1–5, 7, 9, and pl. 2, fig. 1 in Jánossy (1981) sub *Francolinus capeki*, and pl. 2, fig. 2 in Jánossy (1981) sub *Perdix perdix jurcsaki*
MEASUREMENTS **DA 2C**: Humerus: distal width = 8.2 mm, carpometacarpus: proximal width = 7.4 mm, tarsometatarsus: distal width = 7.9 mm, 8.1 mm. **DA 4B**: Humerus: proximal width = 11.4 mm, carpometacarpus: length = 22.4 mm, 23.7 mm, 26.1 mm, proximal width = 6.6 mm, 6.9 mm, 7.4 mm, 6.8 mm, distal width = 4.2 mm, 4.2 mm, 5.4 mm

REMARKS. Jánossy (1981: 379) mentioned, that he had at disposal 15 bones or bone fragments of this species from DA 4B and DA 2C, but listed only 12 of them. Of the latter specimens, the following ones are missing from the collection: 2 complete humeri, 1 humerus fragment, 1 ulnar fragment, and 1 tarsometatarsus. The existence and identity of most of these bones, but of one unspecified humerus fragment, was confirmed by photos in Jánossy (1981), so that I included them in the "Material" section. The missing humerus fragment was not included in the list. On the other hand, the carpometacarpus from DA 4B was found in the new material, which was not at disposal for Jánossy.

Pliocene and early Pleistocene localities of Central Europe yielded numerous remains of small phasianids, usually identified as extinct francolins from the modern genus *Francolinus* Stephens, 1819 (Lambrecht 1933, Jánossy 1974a, 1976, 1981, 1985, 1992, Mourer-Chauviré 1993). Mlíkovský (1995) showed, that these bones do not belong to francolins, but to small quails, to which the generic name *Plioperdix* Kretzoi, 1955 was applied, following Bocheński & Kuročkin (1987). Further research showed, that the latter genus is identical with *Palaeocryptonyx* Depéret, 1892, described from the early Pliocene of France (Mlíkovský 1996a: 805, and unpub. results). Mlíkovský (1995) recognized three species of *Plioperdix*, of which *Plioperdix capeki* (Lambrecht, 1933) is both morphologically and metrically identical with *Palaeocryptonyx donnezani* Depéret, 1892. The latter name has precedence. Full revision of the Plio-Pleistocene quails of Europe and adjacent parts of Asia will be given elsewhere (Mlíkovský in prep.). The relevant genus-group name *Lambrechtia* Jánossy, 1974a is a nomen nudum (see Mlíkovský 1992: 458).

Jánossy (1981) identified distal parts of three tarsometatarsi from DA 2C as those of *Perdix perdix jurcsaki* Kretzoi, 1962. The tarsometatarsi differ from the same element of *Perdix* and agree with that of *Palaeocryptonyx* in having the trochlea for digit IV laterally smooth. Hence, they are attributed here to the latter genus and, according to their size, to *Palaeocryptonyx donnezani*. *Perdix perdix jurcsaki* must be deleted from the avifaunal list of Deutsch-Altenburg.

Table 1 Early Pleistocene birds of Deutsch-Altenburg 4B, and Deutsch-Altenburg 2C1 MNI = minimum numbers of individuals

	DA 4B			DA $2C_1$		
	Bones	MNI	% MNI	Bones	MNI	% MNI
Falco tinnunculus	2	1	4.8	–	–	–
Tetrao tetrix	–	–	–	2	1	11.1
Palaeocryptonyx donnezani	17	4	19.0	9	3	33.3
Glaucidium passerinum	1	1	4.8	–	–	–
Aegolius funereus	–	–	–	3	2	22.2
Picus viridis	1	1	4.8	–	–	–
Dendrocopos major	1	1	4.8	–	–	–
Hirundo rustica	8	3	14.3	2	2	22.2
Luscinia sp	3	3	14.3	–	–	–
Turdus (large species)	1	1	4.8	–	–	–
Turdus (middle sized species)	5	3	14.3	1	1	11.1
Garrulus glandarius	2	1	4.8	–	–	–
Coccothraustes coccothraustes	1	1	4.8	–	–	–
Emberiza sp	1	1	4.8	–	–	–
14 species	43	21	100.0	17	9	100.0

Strigidae

Glaucidium passerinum (Linnaeus, 1758)

MATERIAL. DA 4B: tarsometatarsus dex.; MNI = 1
FIGS. Pl. 2, fig. 3 in Janossy (1981).

Aegolius funereus (Linnaeus, 1758)

MATERIAL. DA 2C: dist. tarsometatarsus sin., 2 dist. tarsometatarsi dex.; MNI = 2.
FIGS. Pl. 2, fig. 5 in Jánossy (1981) sub *Athene* cf. *veta*.

REMARKS. Only one of these tarsometatarsi was available to Jánossy (1981), who identified it as that of *Athene* cf. *veta* Jánossy 1974a, described from the late Pliocene of Rębielice Królewskie 1 in Poland (see also Jánossy 1992). The tarsometatarsus differs from the same element of *Athene* and agrees with that of *Aegolius* in being more robust, and in having differently shaped digital trochleae. Hence, *Athene* cf. *veta* should be deleted from the avifaunal list of Deutsch-Altenburg. It should be noted, that also the holotypical coracoid of *Athene veta* belongs to the modern *Aegolius funereus* (see Mlíkovský 1992).

Picidae

Picus viridis Linnaeus, 1758

MATERIAL. DA 4B: dist. tibiotarsus sin.; MNI = 1

Dendrocopos major (Linnaeus, 1758)

MATERIAL. DA 4B: tarsometatarsus dex.; MNI = 1.
FIGS. Pl. 2, fig. 4 in Jánossy (1981) sub *Dendrocopus* [sic!] *submajor*

REMARKS. Jánossy (1981) attributed this tarsometatarsus to *Dendrocopus* [sic!] *submajor* Jánossy 1974b, originally described from the middle Pleistocene of Hundsheim as a subspecies of the modern *Dendrocopus* [sic!] *major*. A restudy of the syntypes of *Dendrocopos submajor* showed that they fall within the variability of the modern *Dendrocopos major*, and that *Dendrocopos submajor* cannot be separated at the species level (Mlíkovský unpub. results). The same is true for the tarsometatarsus from DA 4B.

Hirundinidae

***Hirundo rustica* Linnaeus, 1758**

MATERIAL DA 4B 2 humeri sin., 2 humeri dex., dist. humerus sin., dist. humerus dex., carpometacarpus dex., MNI = 3 DA 2C humerus dex., prox. humerus dex.; MNI = 2
FIGS. Pl. 2, fig. 7 in Jánossy (1981)

Turdidae

***Luscinia* sp.**

MATERIAL DA 4B: 3 prox. humeri sin., MNI = 3.
FIGS. Text-fig. 5 in Jánossy (1981)

REMARKS. Jánossy (1981) attributed two of these humeral fragments to *Sylvia* sp., while the third one was not available to him. The fragments considerably differ from the same element of *Sylvia* and other sylviids, and agree with those of *Luscinia*, in the configuration of the anconal surface of the head, and in the shape of the deltoid crest. The bones fall in the size class of the modern *Luscinia svecica* (Linnaeus, 1758) and *Luscinia cyane* (Pallas, 1776), and cannot be identified at the species level. *Sylvia* sp. must be deleted from the avifaunal list of Deutsch-Altenburg.

***Turdus* sp.** (large species)

MATERIAL DA 4B dist. humerus sin., MNI = 1.

REMARKS. This specimen is of the size of the same element of the modern *Turdus pilaris* Linnaeus, 1758 and *Turdus viscivorus* Linnaeus, 1758, which cannot be properly discerned on the basis of their humeri. Jánossy (1981) tentatively identified the humerus from DA 4B as belonging to *Turdus viscivorus*, which is unsubstantiated.

***Turdus* sp.** (medium sized species)

MATERIAL. DA 4B: 2 prox. humeri sin., 2 prox. humeri dex., dist. humerus sin., MNI = 3 DA 2C: dist. humerus sin., MNI = 1
FIGS. Pl. 2, fig. 10 in Jánossy (1981) sub *Turdus* cf. *philomelos*

REMARKS. These humerus fragments agree in size with the same elements of the modern *Turdus philomelos* Brehm, 1840 and *Turdus merula* Linnaeus, 1758, which cannot be properly discerned on the basis of their humeri. Jánossy (1981) identified those from DA 4B as *Turdus philomelos*, which is overoptimistic.

Corvidae

***Garrulus glandarius* (Linnaeus, 1758)**

MATERIAL. DA 4B. humerus dex., dist humerus sin , MNI = 1
FIGS Pl 1, fig 9, and pl. 2, fig. 13 in Jánossy (1981).

REMARKS. Jánossy (1981) mentioned only one complete humerus of this species, but I found in the box two fragments.

Fringillidae

***Coccothraustes coccothraustes* (Linnaeus, 1758)**

MATERIAL. DA 4B. prox humerus dex , MNI = 1
FIGS Pl 2, fig 11 in Jánossy (1981) sub *Pinicola* sp.

REMARKS. Jánossy (1981) identified this specimen as belonging to "*Pinicola* sp. (cf. *enucleator*)", but the humerus differs in having: (1) median crest more robust, (2) pneumatic fossa more closed, (3) deltoid crest more flaring and more robust, and (4) shaft more robust. *Pinicola* sp. must be deleted from the avifaunal list of Deutsch-Altenburg.

Emberizidae

***Emberiza* sp.**

MATERIAL. DA 4B prox humerus dex ; MNI = 1
FIGS Pl 2, fig 12, and text-fig 7 in Janossy (1981) sub Serinus sp.

REMARKS. Jánossy (1981) identified this humerus as belonging to the genus *Serinus*, identifying it alternatively as "*Serinus* cf. *canarius*" (p. 378), "*Serinus* aff. *serinus*" (p. 385), and "*Serinus* sp." (pp. 385, 388). The bone markedly differs from the same element of *Serinus* and other fringillids, and agrees with that of *Emberiza*, in having the deltoid crest less flaring. The drawing of this humerus fragment in Jánossy (1981, text-fig. 7) is very inaccurate, not resembling the specimen. *Serinus canarius*, *Serinus serinus*, and *Serinus* sp. must be deleted from the avifaunal list of Deutsch-Altenburg. The *Emberiza* bunting from Deutsch-Altenburg was very small, approximately of the size of the modern *Emberiza pusilla* Pallas, 1776.

DISCUSSION

Taxonomy

The restudy of avian remains from Deutsch-Altenburg resulted in several taxonomic changes. Hence, *Perdix perdix* and *Athene veta* must be deleted from the avifaunal list of Deutsch-Altenburg 2C, and the following species must be deleted from the avifaunal list of Deutsch-Altenburg 4B: *Francolinus capeki*, *Dendrocopos submajor*, *Sylvia atricapilla*, *Turdus viscivorus*, *Turdus philomelos*, *Turdus musicus*, *Sitta europaea*, *Sitta* sp., *Serinus serinus*, *Serinus canaria*, *Serinus* sp., and *Pinicola enucleator*. Most of the bones were re-assigned to other genera or even families, or were considered indeterminate at the species level (*Turdus* spp.). The reasons were explained above. In addition, three distal fragments of tarsometatarsi were assigned by Jánossy (1981) to two different *Sitta* species. I consider these fragments indeterminate within the Passeriformes.

Taphonomy
The avian faunas from Deutsch-Altenburg 4B and 2C are rather similar to each other, and can be treated as a unit here, although 4B is younger than 2C (Rabeder 1981). Their taphonomic origin can be mostly credited to one or more small species of owls or raptors. Both *Glaucidium passerinum* and *Aegolius funereus*, which were recorded from 4B and 2C, respectively, could have contributed to the avian assemblage found in Deutsch-Altenburg, but some of the remains (*Palaeocryptonyx donnezani* in particular) are too large for these small owls, so that the presence of a larger owl or raptor at Deutsch-Altenburg is probable.

Ecology
Most of the birds found (60% and 44% in 4B and 2C, respectively) are inhabitants of forests. Species typical for both coniferous (*Glaucidium passerinum*, *Aegolius funereus*) and broadleaved (*Coccothraustes coccothraustes*) forests are represented. Some of the species (*Falco tinnunculus*, *Tetrao tetrix*, and probably *Palaeocryptonyx donnezani*) required open places, but small patches of them would be sufficient for all the three species. Hence, Hainburg Hills were probably largely covered with mixed forests in the early Biharian.

Biogeography
All of the identified modern bird species are typical for boreal parts of the western Palearctic, and all still occur in Central Europe, although their distribution there may be rather patchy (e. g., *Glaucidium passerinum*, *Aegolius funereus*, *Luscinia* sp.). Only one species, *Palaeocryptonyx donnezani*, became extinct. This small quail was widespread in what is now western Palearctic from the middle Pliocene till the end of the Biharian (Mlíkovský 1995, 1996a,b, in prep.).

Paleopathology
None of the identified bones showed any signs of injuries or pathological changes.

REFERENCES

Bochenski Z & Kurochkin E N. 1987: New data on Pliocene phasianids (Aves Phasianidae) of Moldavia and S Ukraine *Acta Zool Cracov* **30**: 81–96.

Depéret C. 1892 Sur la faune d'Oiseaux pliocènes du Roussilon *C R Acad Sci (Paris)* **114** 690–692.

Depéret C 1897: Les animaux pliocènes du Roussilon. *Mém Soc Géol France (Paléontol)* **3** 1–198.

Grayson D.K 1984 *Quantitative zooarchaeology*. Orlando Academic Press, 202 pp

Horaček I. & Ložek V 1988. *Palaeozoology and the Mid-European Quaternary past scope of the approach and selected results* Praha Academia, 102 pp

Janossy D 1974a Upper Pliocene and Lower Pleistocene bird remains from Poland. *Acta Zool Cracov* **19**: 531–566

Janossy D 1974b Die mittelpleistozane Vogelfauna von Hundsheim (Niederösterreich) *Sitzungsber Osterr Akad Wiss (Math -Naturwiss Kl)* **182**. 211–257

Janossy D. 1976 Plio-Pleistocene bird remains from the Carpathian basin I. Galliformes 2. Phasianidae *Aquila* **83**. 29–42

Janossy D 1981. Die altpleistozänen Vogelfaunen von Deutsch-Altenburg 2 und 4 (Niederosterreich) *Beitr Palaont Osterr* **8** 375–391.

Janossy D 1986 *Pleistocene vertebrate faunas of Hungary*. Budapest. Akadémiai Kiadó & Amsterdam Elsevier, 208 pp.

Janossy D 1992: Lower Pleistocene bird remains from Beremend (S-Hungary, Loc 15 and 16.). *Aquila* **99**: 9–25.

Kretzoi M 1955. [Phogallus Gaillard 1939 and Phogallus Tugarinov 1940] *Aquila* **59–62** 367 (In Hungarian)

Kretzoi M 1962 [Avian remains from the early Pleistocene fauna of Betfia] *Aquila* **67–68**: 167-174 (In Hungarian)

Lambrecht K 1933 *Handbuch der Palaeornithologie*. Berlin: Gebr. Borntraeger, 1024 pp

Mais K & Rabeder G 1979: Das Karstgebiet der Hainburger Berge. *Veröff Naturhistor Mus Wien (N F)* **17**. 51–63

MLIKOVSKY J 1992 The present state of knowledge of the Tertiary birds of Central Europe In CAMPBELL K E (ed) *Papers in avian paleontology honoring Pierce Brodkorb Nat Hist Mus Los Angeles Co (Sci Ser)* **36** 433–457

MLIKOVSKY J 1995 Early Pleistocene birds of Stránská skala I Musil's talus cone In MUSIL R (ed) *Stranska skala Hill Excavations of open-air sediments 1964–1970 Anthropos (Brno)* **26** 111–126

MLIKOVSKY J 1996a Tertiary avian faunas of Europe In MLIKOVSKY J (ed) *Tertiary avian localities of Europe Acta Univ Carol (Geol)* **39** 777–818

MLÍKOVSKY J 1996b Early and middle Pleistocene birds from the Bohemian Karst, Czech Republic *Acta Soc Zool Bohem* **60** 187–190

MOURER-CHAUVIRE C 1993 The Pleistocene avifaunas of Europe *Archaeofauna* **2** 53–66

RABEDER G 1972 Eine fossile Hohlenfauna aus dem Steinbruch Hollitzer bei Bad Deutsch-Altenburg (NO) *Hohle* **23** 89–95

RABEDER G 1973 Weitere Grabungsergebnisse von der altpleistozanen Wirbeltierfundstelle Deutsch-Altenburg 2 *Hohle* **24** 8–15

RABEDER G 1981 Die Arvicoliden (Rodentia, Mammalia) aus dem alteren Pliozan und Pleistozan von Niederosterreich *Beitr Palaont Österr* **8** 1–373

VOOUS K H 1977 *List of Recent Holarctic bird species* London Academic Press, 85 pp

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BOOK REVIEW

WESTHEIDE W & RIEGER R (eds) **Spezielle Zoologie. Erster Teil: Einzeller und wirbellose Tiere** Stuttgart, Jena, New York Gustav Fischer Verlag, 1996 XXI + 909 pp Format 190×268 mm Hardcover, price DM 148 – ISBN 3-437-20515-3

Both editors are professors – at University in Osnabruck (Germany) and at Leopold Franzens-University in Innsbruck (Austria) The list of contributors comprises another 23 acknowledged experts affiliated with institutes for zoology and biology mostly in Germany and also in other countries (Austria, Bermudas, Netherlands, USA) As stated in the preface, description of magnificent diversity of animal organisms and their developmental stages, characterization of principal structures and functions, systematic arrangement into groups and categories considering evolutionary approaches – it is in no way a simple undertaking for a one-volume textbook As structural pattern for this treatise served the textbook of zoology edited in 1980 by Wurmbach und Siewing The editors point out that the most difficult problem for the arrangement of this book was a formal presentation of systematic classification regarding consequent phylogenetic concepts At the present time, many parts of the system are matter of controversial dispute Two introductory general chapters present important terms and schemes of phylogenetic systematics and a vocabulary-like list of most significant Latin and Greek verbal elements of zoological names and terms Following text embraces two major groups of animals unicellular eukaryotes – protozoans and multicellular animals – metazoans Working classification schemes presenting categories in hierarchic classification are listed in this textbook using the numerical (decimal) system – without introduction of nomenclatural terms of taxa as usual in textbooks of systematic zoology (e g phylum, class, order, etc) The nomenclature of taxonomical units is given by scientific (Latin) and vernacular (German) names Protozoans (compiled by K Hausmann and N Hulsmannn) are presented when discussing general characters of principal cell structures locomotory organelles and locomotion, modes of energy uptake by mitochondria and plastids, transport systems, multiplication and life cycles, and principles of systematics Systematic overwiew introduces here 15 major protozoan assemblages constructed according to novel approaches to molecular and phylogenetic biology Long-favoured traditional Butschlian classification scheme of protozoa (1880–1889) and also the classification promoted by the Society of Protozoologists (1964) and newly revised by Levine et al (1985) seem to be no more relevant Metazoans are outlined here in 5 major assemblages (taxa) Parazoa (R Rieger), Placozoa (A Ruthmann), Mesozoa (G Haszprunar), diblastic Eumetazoa (R Rieger) and triblastic Eumetazoa – Bilateria (R Rieger) Last-named assemblage includes the Spiralia (W Dohle), Articulata (W Westheide), Euarthropoda (H Paulus), Mandibulata (H K Schminke), Antennata (W Dohle), Nemathelminthes (S Lorenzen), Tentaculata (K Herrmann) and Deuterostomia (R Rieger, W Westheide) The rest of authors provides access to subordinated taxa within the conceptual framework of the above-mentioned major assemblages Particular animal groups are characterized by descriptions of tissues and organ systems, multiplication and development, and by an overview of systematics with significant attention centred on novel approaches to molecular systematic classification Phylogenetic relationships and ultrastructural data in assemblages of metazoans are examined in a similar manner as in protozoans For example parasitic platyhelminths at the end of their free-living larval stage cast off their ciliated epidermis and replace it by peripheral syncytium – neodermis = tegument Derived from neodermis emerged the name of a new taxon Neodermata including the flatworms Trematoda with aspidobothriids and digeneans, and Cercomeromorpha including monogeneans and cestodes The acanthocephalans are classified here within the assemblage of Nemathelminthes (Aschelminthes) Reader specialized in other groups of invertebrates will find most probably additional examples of novel approaches concerning systematic classification Textual part is concluded by a comprehensive list of literature comprising general textbooks and handbooks, and monographs and journal quotations covering particular taxa of invertebrate animals Finally, an extensive index summarizes special zoological terms and taxonomic names This most remarkable volume is amply illustrated by a wealth of 1167 precise figures composed of macro- and microphotographs, and schematic line drawings featuring protozoan and metazoan organisms and their developmental stages as complex unities or external and internal structural parts and organ systems – also in three-dimensional diagrammatic models Further presented are phylogenetic dendrograms (braching diagrams) and relationships, metamorphosis, life cycles, and many more In addition, there are 5 summary-type tables This new textbook on special zoology presents a teamwork of accredited experts specialized in particular systematic groups of invertebrate animals It is set to become an essential reference source for pre- and postgratuate students and lecturers in general and applied zoology as well for life scientists of various profiles Moreover, it may be of practical value for medical and veterinary professionals interested in medical and veterinary zoology with special regard to protozoology and helminthology, entomology and malacology The second volume of this textbook will cover vertebrate animals

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Abstract The offspring of crosses between male black grouse (*Tetrao tetrix*) and female capercaillie (*T. urogallus*) are the most common grouse hybrids. Some male hybrids (F_1 generation) may be fertile and produce offspring (F_2 generation) with females of capercaillie, rarely, with black grouse. Specimens and descriptions of lekking behaviour are also available for probable F_3 and $F_{>3}$ hybrids. We documented 3 and 2 male F_1 hybrids simultaneously displaying on a black grouse lek in Norway (1993–1997), and, solitarily displaying hybrids on black grouse lek in the Czech Republic (1960–64), in Sweden (1991–93) and Norway (1992, 1997). In 1996 and 1997 up to three hybrids were observed on a capercaillie display ground 2 km away from the first mentioned black grouse display ground. Mating with female capercaillie was observed in 1992 and 1994. We describe the hybrids' lekking behaviour and attitudes towards other tetraonids.

Lekking behaviour, backcrossing, grouse hybrids

INTRODUCTION

Hybrids between male black grouse and female capercaillie are the most common grouse hybrids, termed "rakkelhane" in Norwegian. Some male hybrids (F_1 generation) may be fertile and produce offspring (F_2 generation) with females of both capercaillie and black grouse. Skin material and descriptions of lekking behaviour also exist for probable F_3 and $F_{>3}$ hybrids. Successively increased fertility is suspected through such backcrossing (Bergman 1940, Höglund & Porkert 1989, Porkert 1995a, Porkert et al. 1996).

Male F_1 hybrids usually occurs solitarily on black grouse display grounds, and act aggressively towards male black grouse. We have found three reports of collectively displaying hybrids. Crown Prince Rudolf (Anonymus 1883) mentioned 4 hybrids displaying on a capercaillie lekking ground in NE Bohemia, of which two supposed F_3-hybrids were shot the same day (cf. Meyer 1887, Klaus et al. 1989, Porkert 1995a). Viht (1987) reported three hybrids displaying in 1971 and 1972 on a black grouse lekking ground with approximately 20 male black grouse in Estonia. Nyström (1990) observed three male hybrids on a black grouse display ground in Sweden. Bjørn Bjerke (pers. com.) observed 2 hybrids and two female capercaillie on a black grouse display ground in 1985 in SE Norway. Here we describe lekking behaviour of hybrids based on our observations of solitarily (Czech Republic 1960–64, Sweden 1991–93, South-Norway 1992 and 1997) and collectively (South-Norway 1993–97) displaying hybrids on black grouse display grounds, and on a capercaillie display ground in 1996 and 1997.

METHODS

Hybrids displaying at the black grouse lek at Øvre Landvik were first documented by Arne Flor in 1992 (Flor 1993a, b) Jan Porkert and Roar Solheim took part in the observations from 1994 and 1995, respectively Observations were made from blinds close to the displaying ground centers, and the birds' behaviour was documented by photography and video taping. Observation days and observed behaviour and interactions between different birds are given in Tab. 1 and 2 Terminology follows Hjorth (1970). In 1997 Asbjørn Lie contributed with one observation day.

RESULTS

During spring 1992 one hybrid was present on the black grouse lek in Øvre Landvik, S. Norway (Fig. 1), whereas during 1993 and 1994 there were 3 hybrids on this lek together with 3 male black grouse, which displayed in parts of the territories of the hybrids. In 1995, 1996 and 1997 the lek contained 2 hybrids and 1–3 male black grouse. In spring 1996 three other hybrids were observed 2 km away on a capercaillie lek with only one displaying male capercaillie. In 1997 one hybrid was displaying in the center of this display ground prior to the copulation period of the capercaillie. A second subordinated male capercaillie was also observed with a non-vocal display close to the center this year. Both capercaillie were dominantly aggressive towards the hybrid, chasing it away whenever it came too close to either of the capercaillies' respective displays centers. During the peak of copulation period, the hybrid's display center was located some 15–20 meters away from the dominant capercaillie. A hybrid (probably a second individual) displayed some 150–200 m north of the capercaillie's display center. One male hybrid (probably a third individual) was also seen on a black grouse display ground 1.1 km NW of the capercaillie lek (cf. Tab. 1 and 2, 1996 and 1997).

We have observed the following patterns of behaviour:

1. Wing-beat display
Upright and standing on ground without moving forward, similar to black grouse (Fig. 2, cf. Porkert et al. 1997: fig. 2, Hjorth 1970: fig 78).

Announcing with "drumming flight" similar to male capercaillie (Fig. 3, cf. Porkert et al. 1997: fig. 3, Hjorth 1970: fig. 58). Drumming flight may be reduced, and may lack vocal sounds or be performed with reduced sound (Porkert et al. 1997).

2. Thin-neck upright
This behaviour is commonly displayed on ground and in trees to demonstrate the dominance of the territory holder (Hjorth 1970). The hybrid cocks stand or slowly move in a posture very similar to the capercaillie thin-necked upright. (Fig. 4, cf. Porkert et al. 1997: fig. 4, Hjorth 1970: fig. 59).

The display song is an individually varying, recurring "crrrrs"-sound, the frequency is mostly 1–2 kHz, but even reaching approximately 4 kHz (Klaus et al. 1989: fig. 26).

3. Upright cum wingdragging, singing and tailtilting is similar to that in capercaillie
The tail is fully fanned and tilted 30–40° sideways towards the female or rival (Fig. 5, Porkert et al. 1997: fig. 6). The sideways tilting is more pronounced than in both capercaillie and black grouse (cf. Hjorth 1970: figs 63b, 64b, 84b; "black grouse never seen to exceed 15°").

4. Aggressive behaviour
Solitarily displaying hybrids are usually highly aggressive towards male black grouse, as documented in all articles describing observations of hybrids on black grouse leks. During the periode 1953–1987, while the extinction and behaviour of both capercaillie and black grouse was studied in Orlické hory Mountains in NE Bohemia, hybrids were present both before and during the disap-

Tab. 1 Observation days and periods on the black grouse lek at Øvre Landvik, showing behaviour of hybrid "rakkelhaner" towards conspecifics, female grouse and male black grouse Explanations 1 = no days; 2 = no rakkelhanner; 3 = no female capercaillie; 4 = no copulations; 5 = no female black grouse; 6 = no copulations; 7 = fights with male conspecifics – no days; 8 = aggression towards male black grouse – no days; * = data from second lek, see text

year, observation periode	1	2	3	4	5	6	7	8	notes	observer & no days
1992										
26 4	1	1	3	>2	0			0		AF 1
1993										
18 4 –4 5	4	2–3	(1)[i]	0	(1)[ii]	0	0	4	i:heard 24 4. ii:heard 4 5.	AF 4
1994										
26 4 –5 5	7	1	1[i]	1[ii]	0		5	6	i.29 4., 1.5	AF 4
									i, ii 5.5	JP 6
21 –23 5	3	3–1	0		0		0	0	mostly quiet in territory	JP 3
30 9	1	2	0		0		0	0	no activity 1 10.	JP 2
1995										
10 –14 4	2	2	0		0		1	?		AF 2
22 4 –4 5	8	2	1[ii](2?)[iii]	0	1[ii](2)[iii]3[iii]	0	?	1+?[iii]	i 24.4 , ii 25.4	AF 6
									iii 26.4.,heard iii.1 5 ,invitation	RS 6
4 –7 5	4	1–2	0		0		0	0	low activity 8 5; rain, no birds	JP 4
10 5	1	2	0		0		0	0		RS 1
1996										
20 –26 4	2	2	0		0		0	1		AF 2
3 –8 5	6	2	0		3[i]–1[ii]	0	0	2[i]	i 4 4.;invitation,fight ii 5 & 7 4 flew over *the lek 6 5 invitation*	JP 6
1997										
26 4	1	2	0		0		0	0	males not simult on lek No. 2 low act	AL 1
3 –4 5	2	1	0		0		0	0	low act only in tree	JP 2
4 5 *	1	1	0		0		0	0		AF 1

pearance of male capercaillies. This so called "rakkel"-phase (1959–64, Porkert 1990, 1995b) represent a special periode in the extinction phase of both species, caused by habitat degradation due to pollution and modern forestry (Porkert 1979, 1980, 1982, 1991a, b). In this period male black grouse, too, became more aggressive and started solitarily displaying (Porkert 1976). The male hybrid's aggression excluded normal black grouse display on or close to the lekking grounds. The same aggressive behaviour was observed on a black grouse lek with one male hybrid at the Grimsö Research Station in Sweden. After the hybrid cock turned up on this lek in 1991, female black grouse disappeared since 1992. In 1993, the hybrid male moved to another lek 1 km away. This is in contrast to our observations on the black grouse lek with collectively displaying hybrids at Øvre Landvik in S-Norway, where a two-level hierarchy between hybrids and male black grouse developed (Porkert et al. 1997). The male hybrids had fixed territories according to their individual status (Fig 1). Male black grouse were allowed to display at close distance when they stayed at the secondary parts of the display ground, sitting in trees or in the thick heather vegetation.

Head and neck "bowing", with a modulated display sounds is the slightest form of aggressive behaviour, resembling wide-necked attitudes cum belching cantus in capercaillie (Porkert et al. 1997: fig. 7, cf. Hjorth 1970: fig. 64).

Fighting with wings beats and/or pecking between hybrids is similar to capercaillie's fighting behaviour (Hjorth 1970: figs 65, 67), and is initiated and occasionally terminated with deep bowing (Porkert et al. 1997: fig. 8) of both rivals. Dominance is terminated through beak fighting (Porkert et al. 1997: fig. 9) or wing beat fighting (Porkert et al. 1997: fig. 10). This fighting behaviour is mostly observed between the hybrids themselves. Fight between a hybrid and the subordinate capercaillie was observed on April 20, 1997 (Tab. 2). Male black grouse avoid confrontations with hybrids by fleeing (Porkert et al. 1997).

5. Matings

Matings with female capercaillie were observed on April 26, 1992 (AF) and on May 5, 1994 (JP, Fig. 7, 8). In 1992 the single present male hybrid (probably one years old, cf. Porkert 1995a, according to plumage characters) was mating several times with two female capercaillies (Flor 1993a, b). In 1994, one female capercaillie was observed on the lek, and mating was seen only once. The hybrid mated like male capercaillie (Fig. 8, cf. Fig. 9, Porkert et al 1997: fig. 12, and Höglund 1957, Couturier & Couturier 1980: pl. LX, Klaus et al. 1989: fig. 39), now and then with a few wingbeats like male black grouse (cf. Porkert 1996, Porkert et al. 1997: fig. 13, and Hjorth 1970: fig. 85, Klaus et al. 1990: figs 28, 29).

On May 1, 1995 and on May 4 & 6, 1996, 1–3 black grouse females were observed inviting to mate. The invitations were probably directed as well to a male black grouse, which was displaying 3–5 m behind the displaying hybrid (Porkert et al. 1997).

Our observations show that in a choice between male hybrids and male black cocks, a female capercaillie prefers to mate with hybrids, whereas a female black grouse prefers to mate with their own species.

On April 20 & 23, 1997, 3 and 6 copulations, respectively, were observed between the dominant capercaillie male and the females. A total of 5 and 8 hens, respectively, were observed on the display center on these two mornings (Fig. 9). In 1996 the observation tent was placed too close to the mating center of the capercaillies, thus forcing the birds to copulate some 20 meters away. The

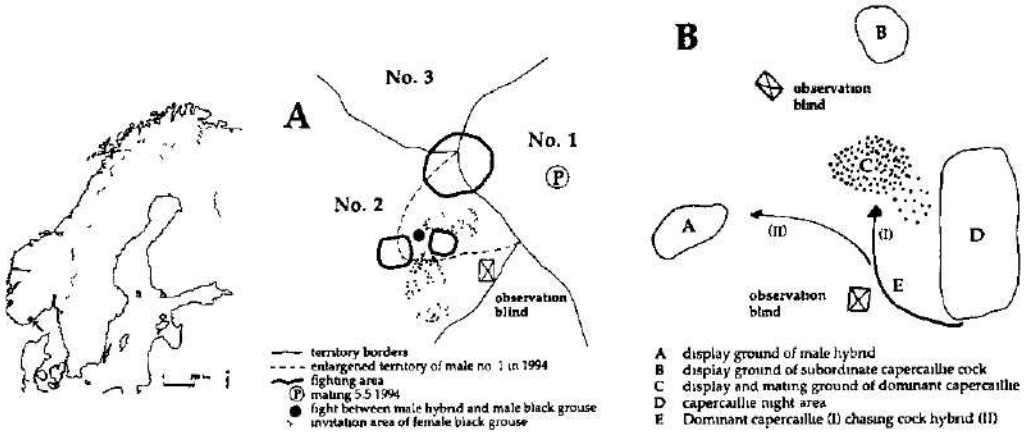


Fig. 1. The location of both the black grouse (A) and the capercaillie (B) display grounds in Øvre Landvik, South Norway, with the territories of the hybrids and the capercaillies

Tab. 2 Observation days and periods on the capercaillie lek at Øvre Landvik, showing behaviour of both hybrid "rakkelhaner" and capercaillie males and females. Explanations: 1 = no days; 2 = no rakkelhanner; 3 = no male capercaillie; 4 = no female capercaillie; 5 = no copulations; 6 = fights with male conspecifics – no observ.; 7 = fights with male capercaillies – no observ.; 8 = fights between capercaillies – no observ.; 9 = capercaillies aggression towards hybrids

year observation periode	1	2	3	4	5	6	7	8	9	notes	observer & no days
1996											
27.4.	1	3	1	5–6	0						AF 1
1.5.	1	1	1	0	0	2	0	0	0		AF 1
9.5.	1	1	1*	0	0	0	0	0		*:only heard	AF, JP 1
21.10.	1	1*								*:only heard	JP 1
1997											
26.3.	1	1	0	0							AF, RS 1
2.–3.4.	2	1	0	0	0	0	0	0			JP 2
13.4.	1	1	1(+1)*	1	0	0	0	0		*:only heard	AF 1
20.4.	1	1	1+1*	5	3	0	1+4*	>3	>4	*:subordinate male	AF 1
23.4.	1	1	1+1	8	6	0	0	>2	>3		AF, RS 1
24.4.	1	0	0	0							RS 1
26 4.	1	0	1	0						birds disturbed by people at 05.00	AF, RS 1
30.4.–2.5.	3	1*	1	0	0	0	0	0	0	*:only heard	

mating center was occupied by the displaying cock hybrid. When the tent was placed at an acceptable distance in 1997, the hybrids was driven away from the original copulation center by both capercaillie males (see map, Fig. 1).

DISCUSSION

Although the hybrid "rakkelhane" was described as early as 1744 (Rutenschiöld in Meyer 1887), and there are many literature reports on hybrids occupying both black grouse and capercaillie display grounds, the hybrids' behaviour has hitherto been fragmentarily described. This is quite contrary to the comprehensive literature on both black grouse and capercaillie (Hjorth 1970, Klaus et al. 1989, 1990, Koivisto 1965, Kruit & Hogan 1967). Here we have described the behaviour of the hybrids according to the terminology used by Hjorth (1970). For a full description of the behaviour patterns, see Porkert et al. (1997).

Contrary to E. Viht's (1987) observations of the female capercaillie which "invited male black grouse only...and was supposed mother of hybrids" on a black grouse display ground with 3 male hybrid "rakkelhaner" in Estonia, no female capercaillie that visited the lek at Øvre Landvik showed any interest for black grouse males (Porkert et al. 1997).

Unfortunately we have been unable to document any F_2-hybrids resulting from the copulations we have observed between hybrids and female capercaillies. This is probably due to at least some of the copulations documented in 1992 (Flor 1993 a, b) being unfulfilled. Both the females capercaillies' repeated invitations and the hybrid male's low age (probably a one year old bird cf. Porkert 1995a for plumage characters) support this interpretation. Contrary to this, the female capercaillie's behaviour on 4 May 1994, indicate a successful copulation with the dominant hybrid (Porkert et al. 1997). However, due to the variable fertility of the hybrids, production of a F_2-generation depend on the sperm quality of the respective male hybrid involved (Höglund & Porkert 1989, cf. Porkert 1995a, Porkert et al. 1996).

E. Viht (1987) pointed out that "female black grouse kept close to male black grouse only", but gave no further information on the relations between females and male hybrids during hens' visit at the lek. Our observations showed that female black grouse exclusively invited male black grouse for mounting. However, due to the presence of the male hybrids, male black grouse were deterred from mating (Porkert et al. 1997). Whereas Hjorth (1994) reports great turbulence on black grouse leks visited by male hybrids, our observations both in NE-Bohemia and in central Sweden show that the aggressiveness of male hybrids did not allow any close presence of male black grouse at all. Only when a highly receptive black grouse hen appears on such a lek occupied by a male hybrid, without any male black grouse present, a successful copulation might be achieved. Thus supposed F_2--hybrids between male hybrid and female black grouse as reported in literature (Meyer 1887, Klaus et al. 1989, Porkert et al. 1996), must be extremely rare. Additional reasons for this are: 1. Copulation by hybrid male with black grouse female may be somewhat more difficult owing to the size difference between the sexes (cf. male capercaillie × female black grouse in the breeding experiment, Höglund & Porkert 1989); 2. Eventually the sperm quality of the respective male hybrid is essential for production of a potential F_2-progeny.

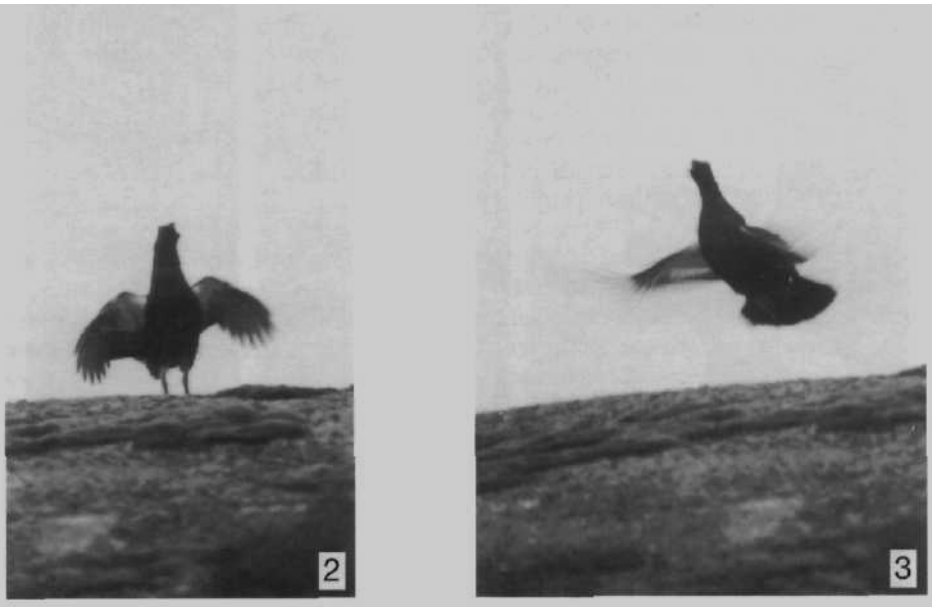
As male hybrids show variation in character, display sounds and probably also fertility (Höglund & Porkert 1989, for weight of testes, see Tab. 2, and unpubl. Data for histology), there is also individual variation in behaviour. We were able to recognize individual male hybrids based on differences in white spots on under-tail coverts and secondaries, on glossy colour and length of tail feathers, as well as display postures and sounds, especially in advertising behaviour. We also noted a specific ability of the birds to modulate their behaviour pattern towards either black grouse or capercaillie respectively (Porkert et al. 1997, cf. Hjorth 1970).

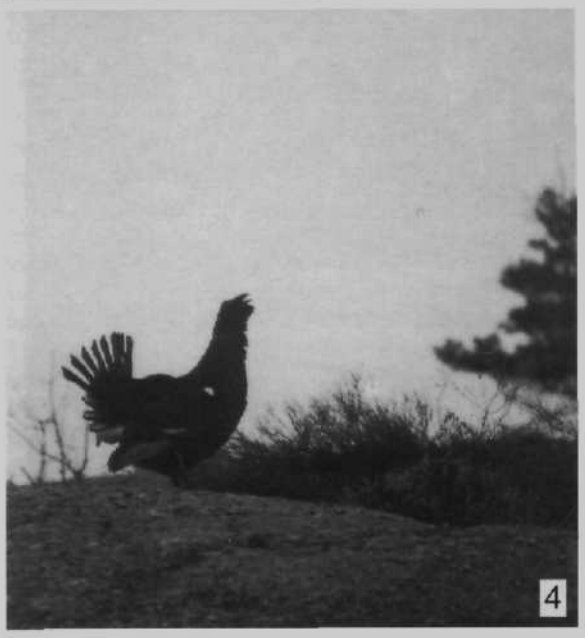
The presence of hybrids is a symptom of skewed sex ratio in capercaillie, in disfavour of males. The number of hybrids has increased in specific areas, first Middle Europe (Porkert 1990), and presently in Fennoscandia (Hjorth 1994 and pers. comm., Porkert 1996 and unpubl., Bakka 1996). Lack of capercaillie males both in small broods in S-Norway (Wegge 1980) and in rest-populations prior to their extinction in Middle Europe (Klaus et al. 1989, Porkert 1990, 1995b) has been recorded as well. The causes relates to interaction between the male capercaillie's morphophysiology and environmental factors. Male capercaillie chicks have a much faster growth rate and retarded flight ability (Kalske & Lindén 1988) during their first summer than female chicks, and are thus prone to higher physiological strain (Lindén 1981, Lindén et al. 1984) and higher vulnerability to predation (Kalske & Lindén 1988). Reduced habital quality is the most likely factor causing such sex-biased growth strain today, and we can see the following possible causes:

1. Acid rain and wind-borne pollutants may have reduced the amount and species diversity of invertebrates available as food for capercaillie chicks (Fimreite 1977, Valeur 1977). Pollution caused vegetation changes in capercaillie habitats where the species later went extinct, especially in dwarf shrubs and gras layer (Porkert 1979, 1980, 1982, 1983, 1991a, b, 1995b, Klaus et al. 1989). The nutritional value of the main foods plants are reduced in the polluted areas and the content of harmful substances (i. e. metals) increase (Porkert 1991b tab. 4, unpubl. data from the Czech Republic and Germany, cf. Klaus et al. 1985).

2. The quality of food plants may be reduced as a result of heavy competitive browsing by very dense ungulate (i. e. moose *Alces alces*, red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) populations. Heavy browsing increase the plants' production of chemical anti-browsing agents, which in turn may have a negative effect on the reproduction of small game like grouse (cf. Selås 1997).

3. By browsing and trampling, dense ungulate populations may also degrade the food plants' (*Vaccinium* and *Filicales*) cover quality for capercaillie chicks as protection against predators and





Figs 2–5. 2 – wing-beat display of male hybrid; 3 – drumming flight of male hybrid; 4 – thin-necked upright display posture of male hybrid; 5 – male hybrid running towards a rival, tilting tail towards him.

Figs 6–9. 6 – male hybrid displaying close to a male black grouse without atacking him; 7 – male hybrid appoaching female capercaillie prior to copulation; 8 – male hybrid begins mating like capercaillie; 9 – male capercaillie mating with females on "mating ground" in 1997, which in 1996 was occupied by a male hybrid (see text).
Figs 2 to 8 Jan Porkert, Fig. 9 Arne Flor.

precipitation, especially prior to development of the chick thermoregulation mechanism (Müller 1982, Porkert 1982, 1983, Klaus et al. 1985, 1989).

4. *Capercaillie habitats are regularly degraded by old forest logging and bog drainage, which* cause habitat fragmentation with many negative effects (Klaus et al. 1989, Rolstad 1989 and others).

Under the lack of the male capercaillies, the mating behaviour of both black cock and capercaillie female (Höglund 1957, Hjorth 1994) favour hybridization. Unfortunately, we are short of information on the fertility of hybrids. Female hybrids are sterile, but some males may reproduce with females of the parent species (Höglund & Porkert 1989, cf. Collett 1906). Male hybrid chicks may have better survival options than male capercaillie chicks, due to slower growth rate during the first weeks after hatching (Höglund & Porkert 1989: Fig. 1). An intermediary diet of hybrids consisting of food components of both parent species (Porkert 1972, Pulliainen 1982), may also give this effect. This may however not counterbalance the hybrids' lower fertility. Females are in general more choosy than males (Hjorth 1970, Höglund & Porkert 1989, cf. Fig. 6 male black grouse mounting a stuffed female capercaillie). The choosiness of female has recently been demonstrated experimentally in flycatchers by Saetre et al. (1997a). In sympatric populations of two related species, female choice even select for divergence in male appearance between the species (Saetre et al. 1997b). However, among birds in general, about one out of ten species has been proved to hybridize with related species, Galliformes being one of the orders with the highest frequencies of hybridization (21.5% of all species hybridize, Grant & Grant 1992). Both capercaillie and black grouse may even produce hybrids with Phasianids (Gray 1958, cf. reference in Höglund & Porkert 1989, Klaus et al 1989). Hybrids of some Darwin's finches in the Galapágos archipelago have even been proven better survivors than their mother species (Grant & Grant 1992). The presence of hybrids in degraded grouse habitats with deteriorated microclimatic conditions may be viewed as a parallell, and a basis for further studies of the survival abilities of "rakkelhons" hybrids and their backcross hybrid progeny in anthropogenetically disturbed habitat s.

CONCLUSION

The behaviour of the "mother" species (capercaillie) dominates the display behaviour of hybrids. But individual variation and flexibility in the modulation of behaviour to suit different situations point to relatively low genetic fixation. Thus both comparison with the behaviour of hybrid F_1--males resulting from male capercaillie × female black grouse crosses, and further backcrossings would be most interesting (cf. i. e. sonogram of display songs from F_1 and F_2 hybrids raised in Boda Viltforskningsstation in Sweden, Höglund & Porkert 1989, described by Klaus et al. 1989, Fig. 26, and supposed F_2–F_3 hybrids observed in nature or found in museum collections, Anon.1883, Meyer 1887, Klaus et al. 1989, Porkert 1995a, Porkert et al. 1996).

Our study area in southern Norway with female capercaillies regularly inviting male hybrids for mating thus present a unique opportunity for field studies of the outcome of such crossings. By the use of radiotelemetric equipment, it should be possible to find potential nests or clutches with F_2--hybrid offspring, and thus record the fitness value of capercaillie and black grouse hybridization. We also stress the need for systematic cross-breeding experiments with capercaillie and black grouse in captivity, to collect accurate data on the hybrids' and later backcrossed progeny's fertility, morphophysiology and genetics.

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REFERENCES

ANONYMUS (Kronprinz Rudolf von Osterreich) 1883: Neue Notizen uber Tetrao medius. *Mitt Ornithol Ver Wien* **7**: 105–109

BAKKA D. 1996: Rackelhonor ett dåligt tecken. *Jaktjournalen* **1996** (November): 50–52.

BERGMAN S. 1940: En korsning mellan rackelhane och tjaderhöna. *Fauna och Flora* **35**: 57–62

COLLETT R. 1906: Hybrids among Norwegian Birds, and their diagnoses. *Christiania Vidensk.-Selsk. Forhandl* **1905**(11): 1–26

COUTURIER M. & COUTURIER A. 1980: *Les coqs de bruyère*. Grenoble, 1529 pp.

FIMREITE N. 1977: Sur nedbør og nedgang i norsk skogsfuglbestand. Foredrag fra Nordisk skogsfuglsymposium 1976. *Viltrapport* **5**: 82–91

FLOR A. 1993a: Rakkelhane parret seg med roy. *Fauna* **46**: 196–197.

FLOR A. 1993b. Biologisk sensasjon in Øvre Landvik. *Liv i Landvik* **2**(5): 377–379.

GRANT P. R. & GRANT B. R. 1992: Hybridization of birds species. *Science* **256**: 193–197

GRAY A. P. 1958. Birds hybrids – a check list with bibliography. Fam. Tetraonidae. *Techn. Comm.* **13**: 79–85.

HJORTH I. 1970: Reproductive behaviour in Tetraonidae with Special Reference to Males. *Viltrevy* **7**: 181–596

HJORTH I. 1994. *Tjadern. En skogsfågel*. Jönkoping. Skogsstyrelsen, 182 pp.

HOGLUND N. H. 1957 [Instinctive activities in captive Swedish Tetraonidae in connection with mating]. *Viltrevy* **1**: 225–232 (in Swedish)

HÖGLUND N. H. & PORKERT J. 1989: Experimentelle Kreuzungen zwischen Auer- und Birkhuhn. (Tetrao urogallus et Tetrao tetrix). *Ztschr. Jagdwiss.* **35**: 221–234.

KALSKE A. & LINDEN H. 1988: Sexual differences in flight ability of capercaillie chicks. *XI Nordic Congr. Game Res. Espoo, Finland. Abstr.* P. 35.

KLAUS S., BOOCK W., GÖRNER M. & SEIBT E. 1985: Zur Ökologie des Auerhuhns in Thuringen. *Acta Ornithoecol. Jena* **1**: 3–46.

KLAUS S., ANDREEV A. V., BERGMANN H.-H., MULLER F., PORKERT J. & WIESNER J. 1989: *Die Auerhühner. Tetrao urogallus und T. urogalloides. Neue Brehm-Bücherei 86. 2. durchges. Aufl.* Wittenberg Lutherstadt: A. Ziemsen Verlag, 280 pp.

KLAUS S., BERGMANN H.-H., MARTI C., MÜLLER F., VITOVIČ O. A. & WIESNER J. 1990: *Die Birkhuhner Tetrao tetrix und T. mlokosewiczi. Die Neue Brehm-Bücherei 397*. Wittenberg Lutherstadt: A. Ziemsen Verlag, 280 p.

KOIVISTO I. 1965. Behaviour of the Black Grouse during the Spring Display. *Finnish Game Res.* **26**: 1–60.

KRUIT J. P. & HOGAN J. A. 1967. Social behaviour of the lek in Black Grouse. *Ardea* **55**: 203–240.

LINDÉN H. 1981: Growth rates and early energy requirements of captive juvenile capercaillie, Tetrao urogallus. *Finnish Game Res.* **39**: 53–67

LINDÉN H., MILONOFF M. & WIKMAN M. 1984: Sexual differences in growth strategies of the capercaillie Tetrao urogallus. *Finnish Game Res.* **42**: 29–35.

MEYER A. B. 1887: *Unser Auer-, Rackel- und Birkwild und seine Abarten*. Wien: A. W. Künast. XII+95 pp., Atlas 17 Tafeln

MULLER F. 1982: Causes de regression du grand tetras en Europe Centrale et les mesures conservatoires à envisage. Pp. 90–111 In. *Actes Coll. Int. Grand Tetras Tetrao urogallus major*. Colmar, 286 pp

NYSTROM H. 1990: *Vallefjall och Larieån*. Göteborg: Tre Böker, 218 pp.

PORKERT J. 1972. Zum Gritwechsel bei unseren Waldhühnern (Tetraonidae). *Věst. Čs. Společ. Zool.* **36**: 134–159

PORKERT J. 1976: Methoden zur Untersuchung der Fortpflanzungsbiologie bedrohter Tetraoniden-Populationen (Aves: Galliformes). *Věst. Čs. Společ. Zool.* **40**: 41–52

PORKERT J. 1979: The influence of human factors on Tetraonid Populations in Czechoslovakia. Pp.. 74–82. In T. W. I. LOVEL (ed.): *Woodland Grouse. Proc. Int. Symp. Grouse 1*. WPA Suffolk, 178 pp.

PORKERT J. 1980: Vergrasung des Waldbodens als Birkwildproblem. *Beih. Veröff. Naturschutz Landschaftspflege Baden-Wurttenberg* **16**: 75–95.

PORKERT J. 1982: Pas de chance de survie du Grands Tetras dans les Sudetes Orientales. Pp.. 120–136. In *Actes Coll. Int. Grand Tetras Tetrao urogallus major*. Colmar, 286 pp.

PORKERT J. 1983: Einge Faktoren, die die Überlebenschancen der Tetraoniden in Ostsudeten beeinflussen. *Proc. XVI IUGB Congr.* Pp.: 668–678

PORKERT J. 1990: Zu Bastardierungen in den Anstiegs- und Aussterbensphasen einiger mitteleuropäischen Populationen des Auerhuhns Tetrao urogallus (Tetraonidae, Aves). *Acta Soc. Zool. Bohemoslov.* **54**: 56–68

PORKERT J 1991a Hoarfrost deposits as a factor contributing to the extinction of tetraonids in the eastern Sudetes In JENKINS D (ed) Proc Int Symp Grouse 5 *Ornis Scand* **22** 292–293
PORKERT J 1991b Nebelfrost als das Aussterben von Tetraoniden fördernder Faktor in den Ostsudeten *Acta Ornithoecol* Jena **2** 195–209
PORKERT J 1995a [Hybrids between Capercaillie (Tetrao urogallus) and Black Grouse (Tetrao tetrix) and their characteristics] *Fauna* **48** 52–61 (in Norwegian)
PORKERT J 1995b Nebelfrostdeposition, Heidelbeerruckgang, Auftreten von Rackelhuhnern-Begleiterscheinungen des Aussterbens von Auerhuhn (Tetrao urogallus) und Birkhuhn (Tetrao tetrix) im Orlicke Hory (Adlergebirge), Tschechien *Naturschutzreport* **10** 173–182
PORKERT J 1996 Dør storfuglen ut i Øvre Landvik? *Liv i Landvik* **3** 261–262
PORKERT J, LIFJELD J T & TORNBERG R 1996 Backcrossings of Tetrao hybrids (T tetrix male × T urogallus female) with their parent species a descriptions of female offspring based on museum skins *Aquilo Ser Zool* **29** 33–41
PORKERT J, SOLHEIM R & FLOR A 1997 Behaviour of hybrid male Tetrao tetrix × T urogallus on black grouse leks *Wildlife Biol* **3** 169–176
PULLIAINEN E 1982 Food selection in the tetraonid hybrids Lyrurus tetrix × Tetrao urogallus, Lyrurus tetrix × × Lagopus lagopus and Tetrao urogallus x Lagopus lagopus *Ornis Fennica* **59** 170–174
ROLSTAD J 1989 *Habitat and range use of capercaillie Tetrao urogallus L in southcentral Scandinavian boreal forests with special reference to the influence of modern forestry* Dr Agric Thesis Ås-NLH
SELÅS V 1997 Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants the mast depression hypothesis *Oikos* **80** 257–268
SALTRE G-P, KRAL M & BUREŠ S 1997a Differential species recognition abilities of males and females in a flycatchers hybrid zone *J Avian Biol* **28** 259–263
SALTRE G-P, MOUM T, BUREŠ S, KRÁL M, ADAMJAN M & MORENO J 1997b A sexually selected character displacement in flycatchers reinforces premating isolation *Nature* **387** 589–592
VALEUR P 1977 Nedgang i skogfuglbestanden i relasjon til sur nedbør Foredrag fra Nordisk skogsfuglsymposium 1976 *Viltrapport* **5** 92
VIHT E 1987 [*The Black Grouse in Estonia*] Tallinn Valgus, 152 pp (in Estonian)
WEGGE P 1980 Distorted sex ratio among small broods in a declining Capercaillie population *Ornis Scand* **11** 106–109

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The embryology of the anterior orbital glands of some squamate reptiles

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Abstract Of the two anterior orbital glands in squamate reptiles, the anterior lacrimal gland and the Harderian gland, only the latter is both ubiquitous and enigmatic. It was suggested that both the development of the Harderian gland and its embryological association with the anterior lacrimal gland differ between the lizard and the mammals. The aim of this study was to examine the organogenesis of the anterior orbital glands of several squamate species, thence determining whether the sole lizard previously examined was representative of the squamata. Both adult and embryos of several species from 4 major squamate lineages (Serpentes, Iguania, Scincomorpha and Gekkota) were examined at the light microscopic level. Though the Harderian glands of these squamates all exhibited the same sequence of events leading to maturation, variation was observed in both the inception of the gland and the association of the gland with other orbital structures. In all cases, the Harderian gland was developmentally associated with the proximal end of the lacrimal canal, either directly (Serpentes) or indirectly (other squamates). Only the Iguanians examined possessed an anterior lacrimal gland, which may have developed from the same primordia as the Harderian gland. It was thus concluded, that not only did the anterior orbital glands of squamates originate from a single glandular primordia, but also that they have done so in close association with the lacrimal canal. Since the lacrimal canal opens distally into the VNO, the combination of both this embryological data and previous morphological observations strongly imply that the gland may function in the vomeronasal sense.

Harderian gland, anterior lacrimal gland, Squamata, lacrimal duct, VNO

There are at most two glands found in the anterior orbit of squamate reptiles: the anterior lacrimal gland and Harderian gland (Fig. 1). When present, the anterior lacrimal gland is a small, mucous secreting structure associated with the anterior conjunctival sac (Saint-Girons 1982). It is presumed to function in orbital lubrication. The structure and function of the Harderian gland, however, is somewhat more controversial. The Harderian gland, originally described in 1694 in the deer, is an orbital feature of most tetrapods closely associated with the nictitating membrane (Cowan 1969, Saint-Girons 1982, Payne 1994). There has been little research on the reptilian Harderian gland. Saint-Girons (1988) suggested that the reptiles, a paraphyletic group of tetrapods, always possess a Harderian gland and may also possess other orbital glands (see Fig. 1). The Harderian gland in reptiles seems to vary in size, with large post-orbital lobes having been described in several species of colubroid snakes (Dullemeijer 1958, McDowell 1969, Savitzky 1978, Saint-Girons 1988). In most lizards, however, the Harderian gland appears to be uniformly smaller (Saint-Girons 1982, Rehorek 1992). The Harderian gland of squamate reptiles has only been described at the light microscopic level (Saint-Girons 1982, 1985, 1988) and a few ultrastructural analyses (Chieffi-Baccari et al. 1990, Minucci et al. 1992, Rehorek 1997b, Rehorek et al. 1997). The sparse knowledge of the structure of the squamate Harderian gland and the lack of ultrastructural analyses at a broad phylogenetic level has led to the assumption that it has a uniform structure and function (Chieffi et al. 1992). The function of the Harderian gland in squamate reptiles is currently unknown. However, there is some

morphological evidence which suggests that it may function as part of the vomeronasal system (Rehorek 1997a, b, Hillenius & Rehorek 1997).

The embryology of the Harderian gland has only been described in a few disparate terrestrial vertebrate species. In the three species of terrestrial frogs thus far studied, the Harderian gland develops during metamorphosis at either the premetamorphic (Shirama et al 1982) or climax (Walls 1942, Kaltenbach et al. 1980, Shirama et al. 1982, Wake 1985) stages. It is thought to develop from the corneal epithelium (Kaltenbach et al. 1980). In the aquatic frog, *Xenopus laevis* Daudin, 1803, the Harderian gland develops at a much later stage (Shirama et al. 1982). This was correlated to the absence of a nictitating membrane. Organogenesis of the Harderian gland in squamates has only been described in the lizard, *Podarcis s. sicula* Rafinesque- Schmaltz, 1810. In this case, the Harderian gland develops prenatally, and appears to be fully developed by birth (Chieffi-Baccari et al. 1995). In both the lab mouse and the lab rat, the Harderian gland appears just before birth, forming as a thickening of the conjunctival epithelium in the internal corner of the eye (Paligová & Pospíšilová 1972, Michael et al. 1988). By birth an immature, non-functional Harderian gland is found at the base of the nictitating membrane in the mouse (Gray 1982, Michael 1988). The Harderian gland in both these rodents and several hamsters matures postnatally (Kelenyi & Orban 1964, Bucana & Nadakavukaren 1972, 1973, Shirama & Hokano 1992, Lopez et al. 1992).

Two major theories were proposed for the evolution of the anterior orbital glands in tetrapods by Sakai (1981). The "migration", or "single gland theory", states that the variable location of the Harderian gland observed is due to the migration of a single gland in the orbital region. This theory was further expanded and supported by Chieffi-Baccari et al. (1992), who proposed that the anterior lacrimal and Harderian glands originated from the same primordium in the lizard *Podarcis s. sicula*, and then separated at a later embryonic stage. Alternatively, the "two glands theory" states that there are two glands, originating from two separate primordia. Morphological variation in position of both the anterior lacrimal and the Harderian gland in mammals led Sakai (1981) to support the latter theory. This was further supported by embryological data from the mouse, wherein the Harderian gland and the anterior lacrimal gland form at different stages during development (Michael et al. 1988). Thus, it seems that there is support for both of these hypotheses, from the Reptilia and Mammalia respectively.

The present study examines the organogenesis of the Harderian gland in several squamate embryos in an effort the determine whether the development of the Harderian gland in *Podarcis s. sicula* (Chieffi-Baccari et al. 1995) is representative of the squamata, despite the morphological differences observed between adults of different families (Rehorek 1997a, b). Once this has been established, the validity of the two hypotheses regarding Harderian gland development will be discussed.

MATERIAL AND METHODS

Specimens of adult lizards (Scincidae *Hemiergis decresiensis* (Cuvier, 1829) n=5; Gekkota *Christinus marmoratus* (Grey, 1848) n=5, Agamidae *Pogona vitticeps* (Ahl, 1926) n=5) and hatchling snake (Elapidae. *Pseudonaja textilis* Demeril. Bibron et Dumeril, 1854) n=3) were obtained from field excursions in South Australia They were killed either by an overdose of sodium pentobarbitol (Nembutal) or anaethesized with chloroform vapours, and subsequently decapitated With the exception of *Pogona vitticeps*, whole heads were fixed in 10% formalin, and 7 micron serial paraffin sections were cut and then stained with Haematoxylin and Eosin Due to the large size of the skull of *Pogona vitticeps*, the Harderian glands were dissected out, and they were then prepared in the same manner as the whole heads.

Embryos from nine species, representing three snake families, were examined from the collection at the Department of Biological Sciences, Old Dominion University, USA These previously serially cut paraffin sections (7 micron) of whole heads had been stained with Haematoxylin and Eosin They had been staged according to Zehr (1962), with at least one specimen available per stage. The following species and stages were examined. Colubri-

dae: *Lampropeltis getulus* (Linnaeus, 1758) [27, 30, 32], *Coluber constrictor* (Linnaeus, 1758) [32], *Nerodia sipedon* (Linnaeus, 1758) [32], *Diadophis punctatus* (Linnaeus, 1766) [22, 24, 26, 27, 28, 30, 32]; Viperidae. *Crotalus horridus* (Linnaeus, 1758) [26, 27, 29, 30, 33], *Agkistrodon piscivorous* (Lacépède, 1889) [28, 29, 31, 32, 34, 35], *A. contortrix* [36], Boidae *Python regius* (Shaw, 1802) [29, 30, 31, 33–35], *P. molurus* (Gray, 1842) [33–35, 37]

Three species of embryonic lizards were examined from the collection at the Faculty of Medicine, Charles University, Plzeň. These previously serially cut paraffin sections (7 micron) of whole heads had been stained with Haematoxylin and Eosin. They had been staged according to total body length, and only one specimen was available per stage. The following species and stages were examined. Lacertidae *Lacerta saxicola* Eversmann, 1834 [6 mm, 7 mm, 8 mm]; Gekkota. *Gekko gecko* Barbour, 1912 [35 mm, 40 mm, 46 mm], Agamidae. *Agama* sp. [17 mm, 20 mm, 22 mm, 23 mm, 25 mm, 28 mm].

Two embryos of *Hemiergis decresiensis*, which had been previously collected and stored in a solution of 3% formaldehyde and 3% gluteraldehyde in phosphate buffer at pH 7.4, were selected and staged according to the standard tables of Dufaure & Hubert (1961). The 7 micron serial paraffin sections of the heads were stained with *Haematoxylin and Eosin*

RESULTS

The organogenesis of the Harderian gland and its relationship to the lacrimal canal in the three families of snakes examined were roughly similiar at the early embryonic stages. No nictitating membrane was observed. At stage 28, the lacrimal canal is first visible, as it buds off from the lateral side of the vomeronasal duct, failing to extend to the orbital region. By stage 29, the lacrimal canal reaches the orbit. Here the Harderian gland intially appears as an invagination of the epithelium in close proximity to the opening of the lacrimal canal (Fig. 2a), and begins to develop into a solid tube. By stage 31, the lacrimal canal is in the process of moving from the lateral to the medial side of the vomeronasal duct. Thereafter, the Harderian gland and its relationship to the lacrimal canal varies among the three groups of snakes studied.

In the colubrids, at stage 32, the Harderian gland appears to be confluent with the lacrimal canal (Fig. 2b). At this stage, the Harderian gland is a semi-solid tube, gradually extending from the conjunctival epithelium into the mesenchymal stroma.

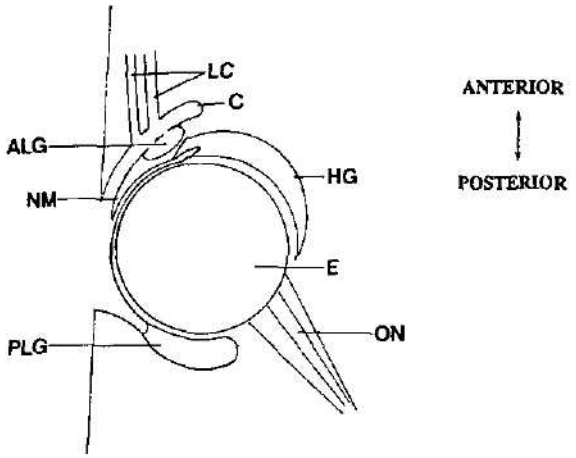

Fig. 1 A schematic diagram of a horizontal section through the orbital region of a reptile. Abbreviations: ALG – anterior lacrimal gland, C – conjunctiva, E – eye, HG – Harderian gland, LC – lacrimal canaliculi, NM – nictitating membrane, ON – optic nerve, PLG – posterior lacrimal gland

In the viperids, at stage 32, the lacrimal canal largely by-passes the conjunctival space, as it passes deep to the eyeball, continuous with the semi-hollow tubules of the Harderian gland. There is a small tubule from the lacrimal canal which opens into the conjunctival space. At stage 33, the Harderian gland is a series of tubes attached to the lacrimal canal. The Harderian gland opens into the orbit independent of the lacrimal canal. The body of the gland gradually expands into the mesenchymal stroma deep in the orbit. At stage 34, the lacrimal canal forms an antechamber before reaching the orbital region, sending off a branch to both the conjunctival region and the Harderian gland. The body of the gland gradually expands into the mesenchymal stroma, which is encapsulated (Fig. 2c). At stage 35, the lacrimal canal bifurcates, producing two canaliculi, which open into the conjunctival space and the Harderian gland respectively. The body of the Harderian gland increases in size as it invades the mesenchymal stroma (Fig. 2d). Some segregation of the acini can be seen at this stage. At stage 36, the lacrimal canaliculi are separate, with the larger medial one opening into the Harderian gland, and the smaller lateral one opening into the orbit. This arrangement is similar to the adult condition.

In the hatchling Elap-id, the individual acini of the Harderian gland are separated by a small amount of interacinar connective tissue (Fig. 2e), as it takes on the appearance of the adult condition. The Harderian gland fills the oral half of the orbit.

In Boids at stage 31, the lacrimal canal opens directly into the Harderian gland. Between stages 33–35, the Harderian gland undergoes rapid development. The Harderian gland opens into the conjunctival region independent of the lacrimal canal. This is similar to the adult condition. By this stage, the Harderian gland comprises a series of tubules, with small lumens, extending deep into the orbital region. The acini of the gland are separated by mesenchymal stroma, and the entire gland is encapsulated. At stage 37, the glandular duct cells can be histologically distinguished from the cells of the glandular body, as the lumen can be now distinguished in most acini (Fig. 2f).

In all lizards examined, the lacrimal canal opens anterior to the Harderian gland, separated from it by the nictitating membrane. However, no nictitating membrane is found in the adult gekkonid. The route of the lacrimal canal in the gekkonid is largely subcutaneous in the adult, and was difficult to find in the embryos.

The gekkonid Harderian gland is present at both 40 and 46 mm stages. Prior to 40 mm only mesenchymal stroma can be seen in that area. By 40 mm, the mesenchymal stroma in the deep orbit contains the dense tubules of the Harderian gland (Fig. 3a), which proliferate and have large lumens by 46 mm (Fig. 3b). There is still a sizeable amount of mesenchymal stroma. In the adult, the acini of the Harderian gland have only a little surrounding connective tissue (Fig. 3c). The Harderian gland is a small, curved structure which is confined to the anterior aspect of the orbit.

As no adult lacertid material could be obtained, adult skink material was veiwed. Both lacertids and skinks have been classified as scincomorphs. In all three stages of the embryonic lacertid, both the Harderian gland and the lacrimal canal are present. The Harderian gland is a series of solid tubules, extending into the mesenchymal stroma (Fig. 3d). By 8mm the lacrimal canal becomes hollow, whilst the Harderian gland remains a mass of tubules, with small lumens and a reduced amount of mesenchymal stroma. At this stage, the development of the Harderian gland approximates that of the adult in size with a minimal amount of interacinar connective tissue. Thus, there is rapid development of the Harderian gland at this time.

The Harderian gland of the skink, *Hemiergis descresiensis*, appears at stage 36 as a thickening of the conjunctival epithelium between the nictitating membrane and the cornea. The Harderian gland in the adult skink is a curved lingual-shaped gland which lies in the midline of the orbit, barely reaching the optic nerve.

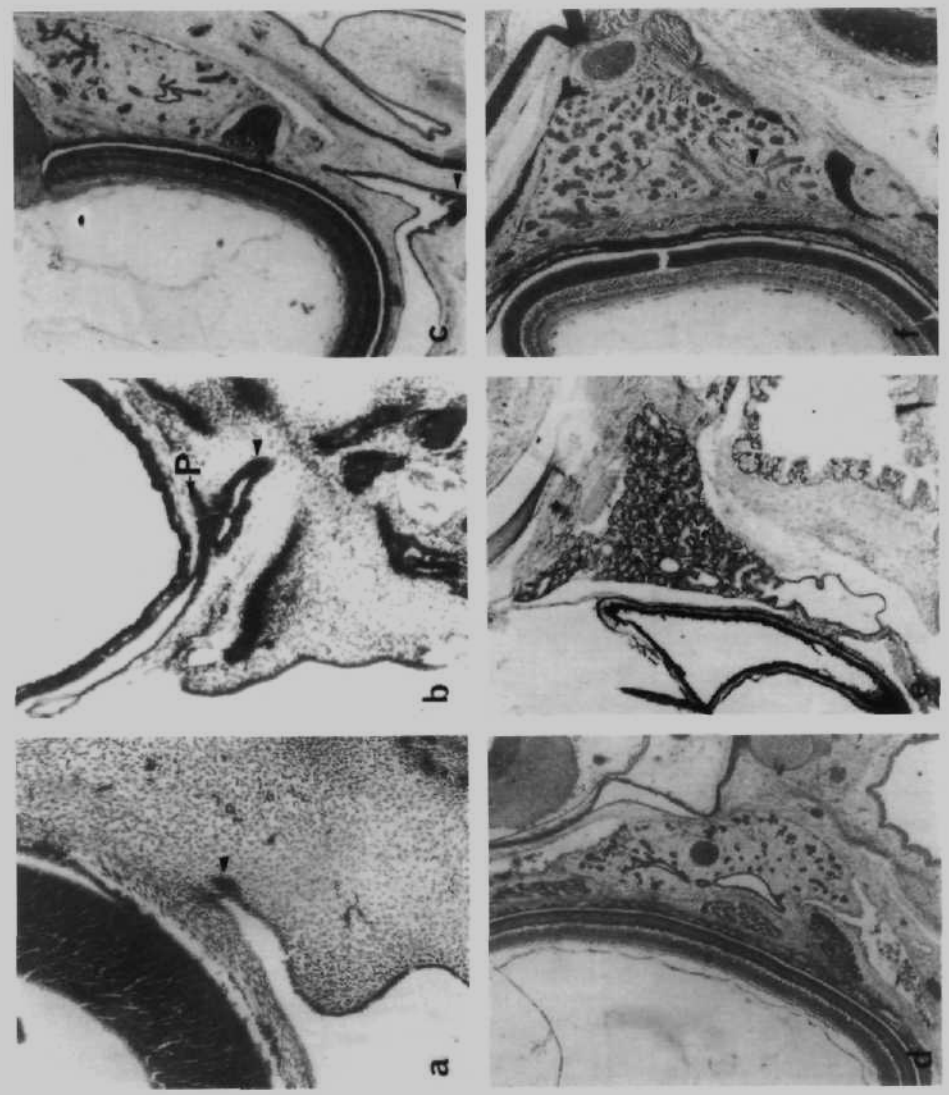

Fig. 2. Light micrographs of transverse sections through snake heads, showing the relationship between the Harderian land and the lacrimal canal. In all cases, the eyeball is situated to the left. a) *Agkistrodon piscivorous* (Viperidae) embryo at stage 29. The lacrimal canal opens into the conjunctival region (arrow head). b) *Diadophis punctatus* (Colubridae) embryo at stage 32. The development of the connection between the lacrimal canal (arrow head) and the Harderian gland primordia (P). c) *Agkistrodon piscivorous* (Viperidae) embryo at stage 34. The lacrimal canl (arrow head) opens into the developping Harderian gland, which is expanding into the encapsulated mesenchymal stroma. d) *A. piscovorous* (Viperidae) embryo at stage 35. e) *Pseudonaja textilis* (Elapidae) postnatal. Little acinar connective tissue present. f) *Python regius* (Boidae) at stage 37. The differentiation of the duct cells (arrow head) from the rest of the cells from of the Harderian gland. Magnification: a = 120×. b = 80×. c = 40×. d = 25×. e = 25×. f = 25×.

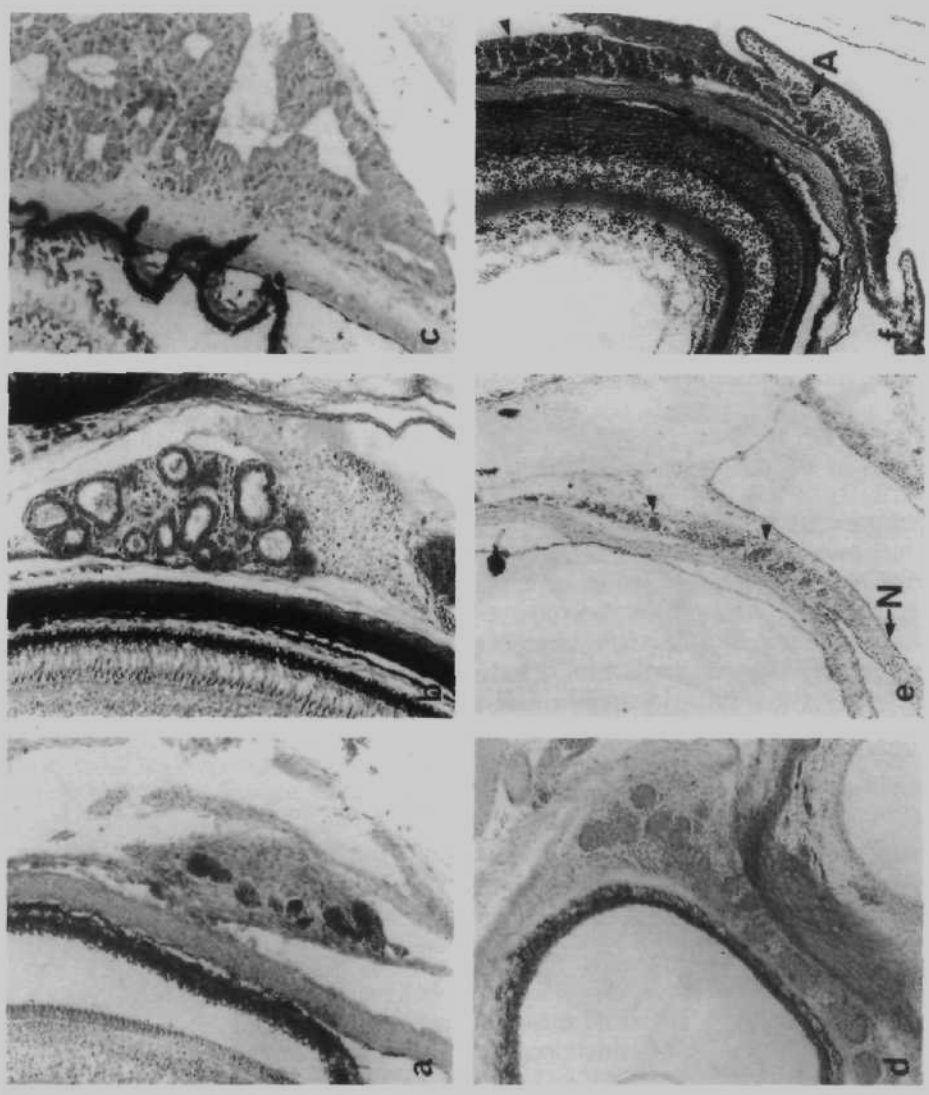

Fig. 3. Light micrographs of transverse sections through lizard heads, showing the development of the Harderian gland in the species studied. In all cases, the eyeball is situated to the left. a) *Gekko gecko* (Gekkota) embryo at 40mm. Solid tubes of the Harderian gland extending into the mesenchymal stroma. b) *G. gecko* (Gekkota) embryo at 46mm. Larger lumens of the Harderian gland acini with less intervening mesenchymal stroma. c) *Christinus marmoratus* (Gekkota) adult. Part of Harderian gland; note the large lumens and the amount of interacinar connective tissue. d) *Lacerta saxicola* (Lacertidae) embryo at 6mm. Developing Harderian gland with extending into the mesenchymal stroma, no lumens in the acini. e) *Agama* sp. (Agamidae) embryo at 17mm. The primordium of the glandular mass (arrow heads) at the base of the nictitating membrane (N). f) *Agama* sp. (Agamidae) embryo at 28mm. Note the morphological separation of the Harderian (arrow head) and anterior lacrimal (A) glands. Magnification: c = 200×, rest = 100×.

The adult agamid, unlike the adult gekkonid and scincomorph, possesses both a Harderian gland and an anterior lacrimal gland. It was difficult to distinguish the two embryologically. They were first present by 17 mm, as a small group of solid tubules attached to the root of the nictitating membrane (Fig. 3e). By 20 mm, the lacrimal canal opens into the conjunctival sac, anterior to the glandular mass. At this stage, it is still difficult to distinguish the two glandular masses. By 28 mm, the anterior lacrimal gland opens onto the conjunctival sac, whereas the Harderian gland opens onto the cornea (Fig. 3f). Though the acini have only small lumens by this stage, it is similar to the adult condition. The Harderian gland of *Pogona vitticeps* is a lingual-shaped structure. It lies in the midline of the orbit and reaches the optic nerve.

DISCUSSION

Previous surveys of Harderian glands in adult squamates have shown some level of morphological diversity (Saint-Girons 1982, Rehorek 1997b). The aim of this survey was firstly to observe the organogenesis of the Harderian gland in a wide range of squamates and secondly to correlate the findings with previous hypotheses regarding the inception of the anterior orbital glands (the anterior lacrimal gland and the Harderian gland).

The sequence of events leading to the maturation of the Harderian gland in the squamates examined is similar to that which has been previously described in *Podarcis s. sicula* (Chieffi-Baccari et al. 1995) and rodents (Mueller 1969, Paligová & Pospíšilová 1972, Bucana & Nadacavukaren 1972, 1973, Vianna & Cruz 1975a, 1975b, Michael 1988, Lopex et al. 1992). However, though the sequence of events leading to maturation are similar, the timing of development differs between squamates and mammals. The results of this study show that the squamate Harderian gland develops mainly prenatally, thereby supporting previous observations (Chieffi-Baccari et al. 1995). Thus, the squamate Harderian gland is potentially function at birth. The significance of this will be discussed later.

There is, however, some variation amoung squamates in both the rate of development of the Harderian gland and the influence of other orbital structures. In general, the lizard Harderian gland develops at a much later stage than that of the snake. Since the staging technique of the lizard embryos examined in Plzeň is incompatible with the staging technique of Dufaure & Hubert (1961), it is difficult to ascertain precisely when the Harderian gland primordium appears. In the skink, *Hemiergis decresiensis*, and the lacertid, *Podarcis s. sicula*, the inception of the Harderian gland occurs during the later embryonic stages (stage 36 out of 40 stages). This also may be the case in *Lacerta saxicola*. Thus, the Harderian gland in scincomorphs appears to develop in the later embryonic stages. No comparably staged material regarding the organogenesis of the Harderian gland has been examined in either agamids or gekkonids. The Harderian gland in snakes, however, is first seen at a much earlier embryonic stage (stage 29 out of 37 stages), thence contrasting with the late development seen in lizards. The much smaller size of the Harderian gland in the adult lizards may be due to its retarded embryonic inception, while the converse may be the case with the snakes.

The development of the Harderian gland in relation to other orbital features also differs between lizards and snakes. In lizards, with the exception of the gekkos, the nictitating membrane develops before the Harderian gland. The association between the nictitating membrane and the Harderian gland has also been observed in both rodents and terrestrial frogs (Paligová & Pospíšilová 1972, Shirama et al. 1982, Michael et al. 1988). However, the nictitating membrane is absent in the aquatic frog, *Xenopus laevis*. This absence has been connected to the retarded inception of the Harderian gland in this species (Shirama et al. 1982).

Both gekkoes and snakes do not possess a nictitating membrane. In neither case does the Harderian gland inception appear to be retarded with respect to the other squamates. Owing to the lack of gekko embryo specimens between 35 mm and 40 mm, the source of invagination leading to the intial development of the Harderian gland in gekkos could not be determined in the present study. Nevertheless, the Harderian gland in the gekko appears to be fully developed at the later embryonic stage. In the snakes, it seems that the presence of the lacrimal canal in the orbit coincides to the inception of the Harderian gland. As discussed previously, the inception of the snake Harderian gland is not retarded, but instead appears at a much earlier embryonic stage.

The lacrimal canal (via lacrimal canaliculi) is proximally connected either directly (snakes and pygopods) or indirectly (other lizards) to the Harderian gland (Bellairs & Boyd 1947, Saint-Girons 1982, Rehorek 1997a). Distally, the lacrimal canal opens into the VNO, or in close proximity thereof (Bellairs & Boyd 1950, Rehorek 1997a). This connection between the orbit (and thus the Harderian gland) and the VNO occurs in other terrestrial vertebrates where all three elements (Harderian gland, lacrimal canal and VNO) are present (Hillenius & Rehorek 1997). It has thus been proposed that the lacrimal canal acts as a conduit for the orbital secretions (Bjerring 1989, Rehorek 1997a, 1997b, Hillenius & Rehorek 1997). The embryology of the lacrimal canal and its relationship to the VNO has been described in several squamate species (Slabý 1979a, b, c, 1981, 1982a, b, c, 1984). Some chamaeleonid lizards lack a VNO (Gabe & Saint-Girons 1976, Slabý 1984), but the lacrimal canal nevertheless terminates in the region of the palate normally occupied by the VNO (Slabý 1984). Examination of embryological material has shown, that the VNO is functional before birth in the garter snake, *Thamnophis sirtalis* Baird et Girard, 1853 (Holtzman & Halpern 1990, 1991a, b) and that the neonate skink, *Eumeces fasciatus* Linnaeus, 1758, is capable of vomerolfaction (Burghardt 1973). Thus, both the developmental and morphological links between the Harderian gland and the lacrimal canal, and between the lacrimal canal and the VNO implies a functional connection between the Harderian gland and the VNO. However, the embryonic relationship between the Harderian gland and the VNO in squamates has not been studied.

The second aim was to ascertain which of the two competeing hypotheses regarding Harderian gland inception was applicable to the squamates. In this study, the presence of two anterior orbital glands (anterior lacrimal and Harderian glands) were found only in the agamids. A common precursor for both the Harderian and the anterior lacrimal glands was found in the unknown species of agamid, and could only be distinguished anatomically as the embryo developed. Thus, the organogenesis of these two anterior orbital glands in both *Podarcis s. sicula* (Chieffi-Baccari et al. 1995) and the agamids supports the "single gland theory". In the embryoes of the other squamates examined, there was no indication of an anterior lacrimal gland. This is despite the presence of small anterior lacrimal glands in adult *Hemiergis descresiensis* (Rehorek 1992). Thus, the absence of multiple anterior orbital glands in the scincomorphs, gekkotans and serpentes could be construed to support the "single gland theory".

In conclusion, it was found that not only did the anterior orbital glands develop from a single primordia, but that the Harderian gland inception did not begin until either the lacrimal canaliculi (Serpentes) or nictitating membrane (Scincomorpha and Iguania) were present in the orbit. The condition in Gekkotans is unresolved. In all squamates, the lacrimal canal is proximally connected (either directly or indirectly) to the Harderian gland, and distally to the VNO. Thus, since the presence lacrimal canal is coincides with the inception of the Harderian gland, and since the lacrimal canal opens distally into the VNO, it is possible that the secretions of the squamate Harderian gland, flowing through the lacrimal canal to the VNO, may have some function in the vomeronasal sense.

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REFERENCES

BELLAIRS A D'A & BOYD J D 1947 The lachrymal apparatus in lizards and snakes 1 The bridle, the orbital glands, lachrymal canaliculi and origin of the lachyrmal duct *Proc Zool Soc Lond* **117** 81–108

BELLAIRS A D'A & BOYD J D 1950 The lachrymal apparatus in lizards and snakes – 2 The anterior part of the lachrymal duct and its relationship with the palate and with the nasal and vomeronasal organs *Proc Zool Soc Lond* **120** 269–310

BJERRING H C 1989 Evolution of the ear duct *Plzeň Lek Sborn, Suppl* **59** 99–108

BUCANA C D & NADAKAVUKAREN M J 1972 Ultrastructural investigation of the postnatal development of the Hamster Harderian gland I Cell Division *Ztschr Zellforsch* **135** 149–153

BUCANA C D & NADAKAVUKAREN M J 1973 Ultrastructural investigation of the postnatal development of the Hamster Harderian gland II Male and Female *Ztschr Zellforsch* **142** 1–12

BURGHARDT G M 1973 Chemical release of prey attack extension to naive newly hatched lizards, Eumeces fasciatus *Copeia* **1973**(1) 178–181

CHIEFFI G, CHIEFFI-BACCARI G, DI MATTEO L, D'ISTRIA M, MARMORINO S, MINUCCI S & VARRIALE B 1992 The Harderian Gland of Amphibians and Reptiles Pp 91–108 In WEBB S M, HOFFMAN R A, PUIG-DOMINGO M L & REITER R J (eds) *Harderian glands Porphyrin metabolism, behavioural and endocrine effects* Berlin Springer Verlag, 325 pp

CHIEFFI-BACCARI G, MINUCCI S, DIMATTEO L & CHIEFFI G 1990 Harderian Gland and Lacrimal Gland of the lizard Podarcis s sicula Histology Histochemistry, and Ultrastructure *Anat Rec* **226** 269–278

CHIEFFI-BACCARI G, DIMATTEO L & MINUCCI S 1995 Organogensis of the orbital glands in the lizard Podarcis s sicula a histological, histochemical and ultrastructural study *Anat Embryol* **192** 43–52

COWAN F B M 1969 *Gross and microscopic anatomy of the orbital glands of Malaclemys and other emydine* turtles *Can J Zool* **487** 723–729

DUFAURE J P & HUBERT J 1961 Table de development du lezard vivipare Lacerta (Zootoca) vivipara Jacquin *Arch Anat Micr Morph Exp* **50** 309–327

DULLEMEIJER P 1958 A comparative functional-anatomical study of the heads of some viperidae *Morph Jahrb* **99** 881–985

GABE M & SAINT GIRONS H 1976 Contribution a la morphologie comparee des fosses nasales et de leur annexes chez les Lepidosauriens *Mem Mus Natl Hist Natur Paris* **98(A)** 1 87

GRAY L E JR, KAVLOCK R J, CHERNOFF N, FERRELL J, MCLAMB J, OSTBY J 1982 Prenatal Exposure to the Herbicide 2,4-Dichlorophenyl-p-Nitrophenyl Ether Destroys the Rodent Harderian Gland *Science* **215** 293–294

HILLENIUS W J & REHOREK S J 1997 Harderian gland and Vomeronasal organ – an ancient collaboration *Amer Zool* 37(5) 60A

HOLTZMAN D A & HALPERN M 1990 Embryonic and Neonatal development of the Vomeronasal and Olfactory Systems in Garter Snakes (Thamnophis spp) *J Morph* **203** 123–140

HOLTZMAN D A & HALPERN M 1991a Incorporation of ^{3}H-Thymidine in the Embryonic Vomeronasal and Olfactory Epithelia of Garter Snakes *J Comp Neurol* **304** 435–449

HOLTZMAN D A & HALPERN M 1991b Incorporation of ^{3}H-Thymidine in Telencephalic Structures of the Vomeronasal and Olfactory Systems of Embryonic Garter Snakes *J Comp Neurol* **305** 450–466

KALTENBACH J C, HARDING C V & SUSAN S 1980 Surface ultrastructure of the cornea and adjacent epidermis during metamorphosis of Rana pipiens a Scanning Electron Microscopic Study *J Morph* **166** 323–335

KELENYI G & ORBAN S 1964 Electron microscopy of the Harderian gland of the rat maturation of the acinar cells and genesis of the secretory droplets *Acta Morph* **13** 155–165

LOPEZ J M , TOLIVIA J & ALVAREZ-URIA M 1992 Postnatal development of the harderian gland in the syrian Golden Hamster (Mesocricetus auratus) A light and electron microscopic study *Anat Rec* **233** 597–616
McDOWELL S B 1969 Toxocalamus, a New Guinea genus of snakes of the family Elapidae *J Zool Lond* **159** 443–511
MICHAEL M I , KHALIL S H MATTA C A & RIZK T A 1988 Normal development of the ocular glands of the mouse *Folia Morph (Praha)* **36** 47–52
MINUCCI S , CHIEFFI BACCARI G & DIMATTEO L 1992 Histology, Histochemistry , and Ultrastructure of the Harderian gland of the Snake Coluber viridiflavus *J Morph* **211** 207–212
MUELLER H B 1969 Die postnatale Entwicklung der Harderschen Druse der weissen Ratte I Lichtmikroskopische Befunde *Ztschr Zellforsch* **100** 421–438
PAYNE A P 1994 The Harderian gland a tercentenial review *J Anat* **185** 1–49
PALIGOVA S & POSPIŠILOVA V 1972 Die perinatale entwicklung der Harderschen druse bei der weissen ratte *Biologia (ČSSR)* **27** 193–202
REHOREK S J 1992 *A comparative morphological analysis of Australian scincid Harderian glands* Unpublished Honours thesis, Adelaide, Australia Univ od Adelaide, iii+84 pp, 20 plates
REHOREK S J 1997a Squamate Harderian gland an overview *Anat Rec* **248** 301–306
REHOREK S J 1997b *A potential role of the squamate harderian gland in vomerolfaction* Unpubl PhD thesis, Adelaide, Australia Univ of Adelaide, iv+123 pp, 23 plates
REHOREK S J , FIRTH B T & HUTCHINSON M N 1997 Morphology of the Harderian gland of some Australian geckos *J Morph* **231** 253–259
SAINT GIRONS H 1982 Histologie comparee des glands orbitaires des Lepidosauriens *Ann Sci Natur Zool Biol Anim* **13** 171–191
SAINT-GIRONS H 1985 Histologie des glandes orbitaires des Crocodiles et des Tortues, et comparaison avec les lepidosauriens *Ann Sci Natur Zool Paris* **13** 249–264
SAINT-GIRONS H 1988 Les glandes cephaliques exocrines des reptiles I Donnees anatomiques et histologiques *Ann Sci Natur Zool Biol Anim* **13**(9) 221–255
SAINT-GIRONS H 1989 Les glandes cephaliques exocrines des reptiles II Considerations fonctionelles et evolutives *Ann Sci Natur Zool Biol Anim* **13**(10) 1–17
SAKAI T 1981 The mammalian Harderian gland morphology, biochemistry, function and phylogeny *Arch Histol Jap* **44** 299–333
SAVITZKY A H 1978 *The origin of the new world proteroglyphous snakes and its bearing on the study of venom delivery systems in snakes* Unpublished PhD thesis, Lawrence Univ of Kansas, viii+387 pp
SHIRAMA K & HOKANO M 1992 Harderian glands and their development in laboratory rats and mice Pp 195–217 In WEBB S M , HOFFMAN R A , PUIG-DOMINGO M L & REITER R J (eds) *Harderian glands Porphyrin metabolism behavioural and endocrine effects* Berlin Springer-Verlag, 325 pp
SHIRAMA K , KIKOYAMA S , TAKEO Y , SHIMIZU K & MAEKAWA K 1982 Development of the Harderian gland during metamorphosis in anurans *Anat Rec* **202** 371–378
SLABY O 1979a Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida I Introduction and morphogenesis of the nasal apparatus in members of the families Lacertidae and Scincidae *Folia Morph (Praha)* **27** 245–258
SLABY O 1979b Morphogenesis of the nasal apparatus in Gecko verticillatus Laur (Family Geckonidae) Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida II *Folia Morph (Praha)* **27** 259–269
SLABY O 1979c Morphogenesis of the nasal apparatus in a member of the family Varanidae Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida III *Folia Morph (Praha)* **27** 270–281
SLABY O 1981 Morphogenesis of the nasal apparatus in Sauropsida IV Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in a member of the family Agamidae *Folia Morph (Praha)* **29** 305–317
SLABY O 1982a Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida V Contribution to knowledge of the early morphogenesis of the nasal apparatus in Teidae *Folia Morph (Praha)* **30** 20–25
SLABY O 1982b Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida VI Morphogenesis of the nasal apparatus of Iguana iguana Shaw and morpholgical interpretation of the individual structures *Folia Morph (Praha)* **30** 75–85
SLABY O 1982c Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida VII Morphogenesis and phylogenetic morphology of the nasal apparatus in Calotes jubatus O B *Folia Morph (Praha)* **30** 238–248

SLABY O 1984 Morphogenesis of the nasal apparatus in a member of the genus Chamelcon L Morphogenesis of the nasal capsule, the nasal epithelial tube and the Organ of Jacobson in Sauropsida VIII *Folia Morph* **32** 225–246

VIANNA G F, CRUZ A R & AZOUBEL R 1975a Mitotic activity and nuclear/cytoplasmic ratio of the lachrymal and Harderian glands of the rat during postnatal life *Acta Anat* **92** 1–7

VIANNA G F, CRUZ A R & AZOUBEL R 1975b Allometric study of the lachrymal and Harderian glands of the rat during postnatal life *Acta Anat* **92** 161–170

WAKE M H 1985 The comparative morphology and evolution of the eyes of caecilians (Amphibia,Gymnophiona) *Zoomorph* **105** 277–295

WALLS G L 1942 The vertebrate eye and its adaptive radiation *Cranbrook Inst Sci Bull* **19**

ZEHR D R 1962 Stages in the Normal Development of the Common Garter Snake, Thamnophis sirtalis sirtalis *Copeia* **1962** 322–329

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Nikolaev G. V. 1987: Plastinčatousye žuki (Coleoptera, Scarabaeoidaea) Kazahstana i Srednej Azii [Scarabaeoidaea (Coleoptera) of Kazakhstan and Central Asia]. Alma-Ata: Izd. Nauka KazSSR, 232 pp. (in Russian).

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